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Genetic variation in the endemic plants of the Athabasca sand dunes: origin, evolution, and implications for conservation

by

Brett Gordon Purdy ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

in

Population Biology

Department of Botany

Edmonton, Alberta

Fall 1995

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February 03, 1994

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May 20th, 1995

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3. Purdy, B. G., and R. J. Bayer. 1995b. Allozyme variation in the Athabasca sand dune endemic *Salix silicicola* and the closely related widespread species, *S. alaxensis*. *Systematic Botany* 20(2): 179-190.
4. Purdy, B. G., and R. J. Bayer. submitted. Genetic variation in populations of the endemic *Achillea millefolium* ssp. *megacephala* from the Athabasca sand dunes and the widespread *A. millefolium* ssp. *lanulosa* in western North America. *Canadian Journal of Botany*.

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Dated: July 24, 1995

"In wilderness I sense the miracle of life, and behind it our
scientific accomplishments fade to trivia"
Charles Lindbergh

Nobody lives here.
Few visit.
The eagle fixes me with a haughty stare.
Within the pines, bruin sniffs, lumbers out, attacks my backpack bearing fruit. I stand rigid, a shout away.
Am I a provider, or a threat? Has he seen people before? Does he care?
Survival.

Sand sifts eastward.
The sandwort, buried beneath, fights upward seeking sun and life.
It succeeds.
The pines are buried. They die. Cones explode. Seeds scatter. Life begins anew.
Survival.

The thrift is mute.
Did it leave kin in distant Skye?
To escape seawater and nibbling sheep?
Is it easier here amid the frigid cold? blasting sand?
Survival.

Elusive cranes, suddenly bold, sweep by low, graceful, haunting calls proud.
First flight for the young.
Survival.

I cross pavement dunes.
My footprints scar the surface. I can't erase them. I've defiled this place.
The eagle stares.
I must take care.

Will it come to this?

The noisy red machine explodes into life. The bear curious looks up.
The rifle cracks. He drops. His life spills rely onto coppery sand.
The cranes panic, flee, tongues shrieking.
The eagle soars from his lofty perch.
Vanishes.

Wheels churn, rip tansy and chickweed kin from the sand below.
They shrivel and do not rise.

Will it come to this?
I must take care.

Ellen Macdonald and Max Macdonald (Borealis, Summer 1991)

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Genetic Variation in the Endemic Plants of the Athabasca Sand Dunes: Origin, Evolution, and Implications for Conservation** by **Brett Gordon Purdy** in partial fulfillment of the requirements for the degree of **Doctor of Philosophy** in **Population Biology**.

Randall J Bayer

Dr. Randall J. Bayer, Supervisor

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Pamela S Soltis

Dr. Pamela S. Soltis, external examiner

Dated: July 24, 1995

Dedication

This thesis is dedicated to my mother and father, Harold and Sheila Purdy, to my wife, Ellen Macdonald, and to my son, Logan Macdonald Purdy, who have all taught me, at one time or another, the important values we should cherish in our lives. A special thanks for all your love and support.

ABSTRACT

In this study, we compared the genetic variation within and among populations of five endemic plant taxa from the Athabasca sand dunes in northern Saskatchewan, Canada, with the related geographically widespread species from which they are thought to have evolved. The results largely conformed with theories and empirical evidence that suggest restricted species have less genetic variation than widespread species. *Stellaria arenicola* and *Deschampsia mackenzieana* have evolved while sympatric with populations of their progenitor species and were found to have less population genetic variation than the widespread species. The tetraploid nature of *Deschampsia mackenzieana* isolated it from the adjacent diploid gene pool of *Deschampsia cespitosa*. In contrast, *Stellaria arenicola* can still hybridize with its progenitor, *Stellaria longipes*, though a shift to higher levels of inbreeding may have aided the evolution of this endemic. Evidence suggests these endemics have evolved from the sympatric gene pool of the progenitor species. *Salix silicicola* and *Armeria maritima* subsp. *interior*, two endemics that have evolved from allopatric arctic progenitors, were found to have less genetic variation than their related widespread taxa. Evidence suggested heterozygosity confers a fitness advantage in the progenitor *Salix alaxensis*, whereas in *Salix silicicola*, a heterozygote deficiency may be due to directional selection or inbreeding. Only one locus in one population was polymorphic in *Armeria maritima* subsp. *interior*, perhaps the rarest endemic on the Athabasca sand dunes, though populations of the progenitor, *Armeria maritima* subsp. *labradorica* were found to have little genetic variation as well. The endemic *Achillea millefolium* subsp. *megacephala*, was found to have more genetic variation than the widespread progenitor, *Achillea millefolium* subsp. *lanulosa*. All of the endemic species had high genetic identity with progenitor populations, regardless of the sympatric or allopatric nature of their respective distributions. These data support previous suggestions that the endemics have evolved on the Athabasca sand dunes during the Holocene. Conservation recommendations were made for preserving the endemic plants and their genetic diversity in light of the information provided from this study.

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I would like to thank Dr. Randy Bayer, my supervisor, for his support and encouragement throughout this project. Our discussions, field work from Arizona to Prudhoe Bay, and time spent around the picnic tables of western North America quenching our thirst have given me much to think about. I would also like to express gratitude to my supervisory committee, changed as it has, from when I started this project in the fall of 1990. The early suggestions of Dr. Greg Henry and Dr. Randy Currah helped set the focus for this project. Discussions with Dr. Dale Vitt and Dr. Bruce Dancik encouraged much thought on the phytogeography and evolution of flora in northern regions. The participation of Dr. Mark Dale, Dr. Curtis Strobeck, and Dr. Pam Soltis was appreciated.

I would also like to thank Shawn Francis, for his help with field work on the Athabasca sand dunes in 1991, which included carrying packs of up to 150 pounds, though we have both vowed never to perform such a task again. Ellen Macdonald, Taiga, and Caora also helped with field work on the sand dunes in 1992. Rod Atton's skillful flying of a C185 Cessena float plane aided the completion of our field work. Harold Purdy provided the sketches of the sand dunes and endemic species found throughout the text of the thesis. My gratitude also goes to the following persons who have, on many occasions, helped me in the past five years: Shunguo Liu, Bernard Goffinet, Barb Thomas, Donna Cherniawsky, Steven Williams, Dr. Ben LePage, Dr. Jim Bassinger, Dr. Geoff Holroyd, and others.

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of Prince Albert, was provided. Their support is gratefully acknowledged. Special thanks to the people of Saskatchewan and the First Peoples of northern Saskatchewan for their efforts to protect the Athabasca sand dunes forever, now designated the Athabasca Sand Dunes Wilderness Provincial Park. One of Canada's gifts of the natural world has been given to the generations of tomorrow.

The inspiration of volunteers and leaders with the Alberta Wilderness Association and other conservation organizations in this province has kept me and others fighting for a piece of the pie, when all that appeared left was crumbs. The personal education achieved by participating in volunteer organizations should never be overlooked. Public speaking, committee work, collaboration, research, conference organization, and media relations, are all life skills that I have been forced to learn, thankfully, from volunteer activities. To Herb Hammond, Stan Rowe, and Radha Batt, thanks for sharing time and thoughts with Ellen and me, you have achieved a vision of life we aspire to live up to - some day we may.

Finally, a special thanks to Dr. Ellen Macdonald, my wife, for her love and support. Ten years ago, Ellen introduced me to the Athabasca sand dunes while completing her Ph. D. in plant ecology at the University of Calgary. Since then, the sand dunes have been our place of spiritual power. Logan, our son, is now our source of inspiration, though the Athabasca sand dunes will always be a place of renewal for our family. Thanks Ellen, for being there, through all the changes of our lives.

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Chapter One
General Introduction

Evolution is fundamentally a genetic phenomenon. Variation among individuals is the basis of evolution. The variation seen within populations is based on three factors: environmental modification, genetic recombination, and mutation. Recombination and mutation are most important for evolution. Random genetic drift and natural selection are two means by which differences are produced in allele frequencies among populations. The technique of characterising alleles by their gene products (allozymes) through gel electrophoresis has provided a means of obtaining empirical data on gene frequencies in populations.

Electrophoretic variation in plants. Over the past two decades, investigations into the genetic structure of plant populations using starch gel electrophoresis have been extensive (*in* Brown, 1979; Loveless and Hamrick, 1984; Hamrick and Godt, 1989). Reviews have attempted to relate ecological, historical and biological parameters of the organisms in question with the amounts and patterns of isozyme variation detected. The aspects most often examined using this approach include phyletic group, life history strategy, geographic range, breeding system, mode of reproduction, and successional status of the species studied.

The Athabasca Sand Dunes

Isozyme variation within species and populations has been found to be as much a function of the individual plant species as it has the historical and biological aspects of the species being investigated. Thus, comparisons among closely related taxa that differ in only a few of these characters have been necessary in any study that attempts to correlate the life history of an organism with measures of genetic variation (Karron, 1987).

In a recent review of the extensive literature on isozyme variation in plants, Hamrick and Godt (1989) found the geographic range of taxa accounted for the largest proportion of variation in species level genetic variation. Species with limited geographic ranges tend to have lower amounts of genetic diversity (Kesseli and Jain, 1984; Warwick and Gottlieb, 1985; Karron, 1987; Karron et al., 1988; Hamrick and Godt, 1989). This reduction of genetic diversity may be due to: (1) chance events such as genetic drift and founder effects; and/or (2) strong directional selection toward genetic uniformity (Karron, 1991). Genetic drift, selection, constraints on gene flow (i.e., loss of alleles or the reduction of polymorphic loci), or inbreeding (i.e., small population size, habitat fragmentation) may influence the genetic structure of populations.

Genetic variation in endemics. Population size and population isolation are major factors influencing the amount and pattern of genetic diversity in natural populations (Franklin, 1980). A fundamental principle of population genetics is that, in closed populations, the existence of only a small number of individuals over several generations will result in a major loss of genetic variation (Wright, 1931; Soulé, 1987). The long term survival of a population is affected by the genetic variation present because of its importance for adaptation to changing environments.

The term endemism, in a classical biogeography definition, does not necessarily imply a small range. Species may be endemic to a particular continent, or region, and not be necessarily rare. The narrow endemic though, is defined by a restricted range and generally is associated with a degree of rarity (Kruckeberg and Rabinowitz, 1985). The restriction of species to a small range may be due to biological, geological, or historical factors.

Recently, biologists have begun investigating the population genetics of species with restricted distributions, such as the narrow endemic. Starch gel electrophoresis has been the most useful technique for the analysis of genetic diversity in endemic taxa. Surveys of allozyme variation in plants have supported theoretical predictions that species with limited ranges and small populations will exhibit low levels of genetic polymorphism (Gottlieb, 1973, 1979; Gottlieb and Pilz, 1976; Levin, Ritter, and Ellstrand, 1979; McLeod et al., 1983; Moran and

Hopper, 1983; Kesseli and Jain, 1984; Warwick and Gottlieb, 1985; McClenaghan and Beauchamp, 1986; Karron et al., 1988; Moran, Muona, and Bell,1989; Pleasants and Wendel, 1989; Bayer, 1989, 1992). Yet, some studies showed that severely restricted populations have maintained almost as much variation as related widespread taxa (Griggs and Jain, 1983; Hiebert and Hamrick, 1983; Gottlieb, Warwick, and Ford, 1985; Bayer and Crawford, 1986; Coates, 1988; Karron et al., 1988; Nickrent and Weins, 1989; Prober et al., 1990; Bayer, 1991; Kuittinen et al., 1991).

Part of the reason for variable results among studies is because of the diversity of species, floristic ages, and enzyme systems investigated. An investigation of patterns of genetic diversity among restricted and widespread species pairs that have evolved in a similar ecosystem for a similar length of time and use similar loci for comparison would overcome some of the problems of many past studies (Karron, 1987, 1991).

The Athabasca sand dunes. Isolated sand dunes are analogous to habitat islands and high rates of endemism have been recorded in such systems (Bowers, 1984). The evolution of species in many sand dune systems has occurred since the Pleistocene glaciations (Bowers, 1984; Pavlik, 1989). High rates of endemism in dune systems have been attributed to adaptation of plants to moving sand and barriers to dispersal and establishment (Bowers, 1984). The boreal forest and arctic tundra have a variety of geologies which have been shown to stimulate speciation (Kruckeberg, 1986), but have very few endemic taxa (Kruckeberg and Rabinowitz, 1985).

In north-western Saskatchewan and adjacent Alberta is a region of active sand dunes and desert-like topography that is unique botanically. Habitats available for plant colonization on the south shore of Lake Athabasca vary from dry blowing sand to relatively stable soil surfaces. The Athabasca sand dunes are a habitat island in the boreal forest and they harbor ten endemic plants that have been classified at specific and subspecific ranks (Raup, 1936; Raup and Argus, 1982; Rowe and Abouguendia, 1982). All but one of these endemic species are restricted to active or stabilized sand dune habitats. The flora of the Athabasca sand dunes represents one of the most important collections of rare and endemic plants in Canada.

Comprising five broad-leaved herbs, four willows, and one grass, the endemic plants of the Athabasca sand dunes are an evolutionary puzzle (Rowe and Abouguendia, 1982). Only two of the endemic taxa have been investigated so far, *Stellaria arenicola* (Macdonald et al., 1987), and *Salix planifolia* subsp. *tyrrellii* (Argus and Steele, 1979). Both of these endemics have evolved sympatric to their parental taxa which occur adjacent to the dunes on the shore of Lake Athabasca. In both studies, greenhouse experiments and reciprocal transplants revealed morphological differences which were genetic in origin and not due to phenotypic plasticity (Argus and Steele, 1979; Macdonald et al., 1987). There are other sand dune endemics which occur both sympatrically and allopatrically to their parental taxa (Argus and Steele, 1979).

The presence of 10 endemic taxa restricted to the Athabasca sand dunes is remarkable as compared to only one other endemic reported in Saskatchewan (Hermesh, 1972) and the low frequency of endemism that characterises the boreal forest biome (Kruckeberg and Rabinowitz, 1985). Conclusions from studies on two of the endemics suggest rapid postglacial evolution of the endemics in sizeable active sand dune areas. Selection pressure and partial genetic isolation have been factors suggested to be important in this evolution (Argus and Steele, 1979; Macdonald et al., 1987).

Characters unique to the endemics such as tomentose leaves and rapid shoot growth could be interpreted as having selective advantages in a shifting sand dune environment. Other endemics (e.g., *Armeria maritima* subsp. *interior*) have characters that distinguish them from closely related parental taxa but that have no obvious selective advantage to the sand dune environment. Founder effects and genetic drift could be responsible for the evolution of this endemic.

There are no published reports on electrophoretic variation in any of the endemics. The sand dunes thus offer a unique opportunity to determine the patterns of genetic diversity among endemic taxa that have evolved in one ecosystem over a similar length of time.

Objectives. The purpose of this study was to provide the first report on amounts and patterns of genetic variation in the endemic taxa of the Athabasca sand dunes. The five sand dune endemics that we included in this study comprise a diverse group of plants having different growth forms, breeding systems, and life history strategies. These plants however, all share one trait, they are restricted to the sand dune habitats on the south shore of Lake Athabasca.

We determined levels of genetic diversity within populations, among populations, and among dune fields. The latter, in effect, represents the entire range of the endemic taxa. The genetic diversity of the parental taxa was also determined as the representation of the gene pool from which the endemics had evolved. From this, we could assess the effects of small population size, restricted distribution, natural selection, or limited gene flow on gene diversity. We could not, however, necessarily determine which of these factors had been most important in structuring the gene diversity in the endemics.

We also made recommendations on the conservation of the endemics and their genetic variation from the available evidence. In a more detailed form, a conservation plan for the endemic plants of the Athabasca sand dunes is being prepared for the World Wildlife Fund Canada and the Saskatchewan Department of Parks and Renewable Resources. Coupling the demographic and genetic information of the populations of endemic plants will reveal areas of high species diversity, relative abundance, and genetic diversity. These areas will be considered most important for the long term protection and evolution of plants on the sand dunes.

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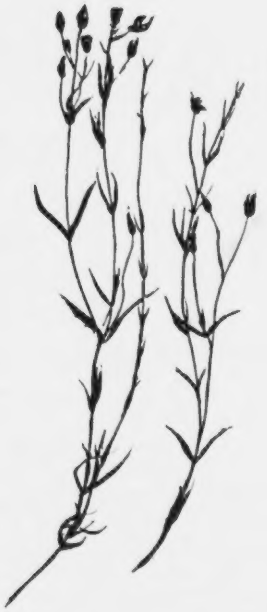
Chapter Two

Genetic variation, breeding system evolution, and conservation of the narrow sand dune endemic *Stellaria arenicola* and the widespread *S. longipes* (Caryophyllaceae) [1]

ABSTRACT. Electrophoretic variation was examined in 14 populations of *Stellaria arenicola*, an endemic of the Athabasca sand dunes in northern Saskatchewan, Canada, and seven populations of *Stellaria longipes*, its progenitor. Three of the *Stellaria longipes* populations were sympatric with the endemic. Populations of the endemic were found to have fewer alleles per polymorphic locus (2.21 vs. 2.37), lower percent polymorphic loci (29.9 vs. 33.8) and lower genetic diversity (0.087 vs. 0.107) than populations of the progenitor. Genetic identities for all pairs of populations were high (0.932 to 1.000). The endemic had one novel allele and shared ten alleles with progenitor populations from the sand dunes that were not found in other populations of *Stellaria longipes*. Most of the genetic variation was found to be partitioned within populations for both species. An investigation of the multilocus outcrossing rates revealed that *Stellaria arenicola* had higher rates of selfing and biparental inbreeding than *Stellaria longipes*. This study suggests that partial genetic isolation through a shift in the breeding system, in addition to previously reported strong directional selection, has been important in the sympatric evolution of the endemic *Stellaria arenicola*. The close genetic relationship between populations of *Stellaria arenicola* and *Stellaria longipes* found on the Athabasca sand dunes supports the suggestion that the endemic evolved while sympatric to the gene pool of the progenitor species that is found presently in the region.

INTRODUCTION



Stellaria arenicola

Populations that are reproductively isolated may gradually exhibit genetic differentiation. For speciation to occur among sexual organisms barriers to gene flow are generally required (Grant, 1981). Sympatric speciation represents a special case in the evolution of new species. There are few studies that have investigated the genetics or ecology of recently evolved sympatric species of plants. Shifts in breeding system accompanied by chromosomal changes (Gottlieb, 1973, 1974; Gottlieb and Pilz, 1976) and strong natural selection (Macdonald et al., 1987) were responsible for the evolution of some sympatric species. Evidence from population genetic studies generally supports the prediction that derivative species will have lower levels of genetic diversity than the progenitor (Gottlieb, 1973, 1974; Crawford and Smith, 1982a, 1982b; Crawford, Ornduff, and Vasey, 1985; Loveless and Hamrick, 1988; Pleasants and Wendel, 1989). If recently evolved sympatric species are still capable of limited gene flow with the progenitor, however, then they have the opportunity to acquire genetic variation from the larger gene pool after speciation has occurred.

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[1] A version of this chapter has been published. Purdy, Bayer, and Macdonald, 1994. *American Journal of Botany* 81: 904-911.

Recently evolved species can often be classified as narrow endemics owing to their restricted geographic ranges. Knowledge of the ecology and genetics of narrow endemics is still limited (Karron, 1987; Pleasants and Wendel, 1989), but could provide relevant information on the fate of rare and endangered species. Plant species with limited ranges generally exhibit lower levels of genetic polymorphism (Karron, 1987; Hamrick and Godt, 1989). This reduced genetic variation has been attributed to strong directional selection, genetic drift, and/or the founder effect (Karron, 1987).

The boreal forest and arctic tundra have a variety of geological features that tend to be correlated with high rates of speciation (Kruckeberg, 1986), but these regions have very few endemic taxa (Kruckeberg and Rabinowitz, 1985). The Athabasca sand dunes in northern Saskatchewan, however, harbor one of the most important collections of rare plants in Canada, including ten endemic taxa (Raup and Argus, 1982). *Stellaria arenicola* Raup (Macdonald et al., 1987) and *Salix planifolia* subsp. *tyrrellii* (Raup) Argus (Argus and Steele, 1979) are the only endemics investigated to date with respect to habitat and morphological differentiation. Both of these endemics have evolved in sympatry with their progenitor taxon, and natural selection and partial genetic isolation have been implicated in their evolution.

The endemic plants of the Athabasca sand dunes provide an excellent opportunity to investigate the role of genetic isolation and natural selection as mechanisms responsible for speciation in sympatric species pairs. This study was conducted to test whether *Stellaria arenicola*, a recently evolved species and a narrow endemic, had lower levels of genetic variation than its widespread progenitor *S. longipes* Goldie. In order to measure the importance of isolating mechanisms in the evolution of the endemic, we evaluated the breeding system of the two species using progeny arrays to estimate the multilocus outcrossing rates. The relationship of *S. arenicola* to populations of *S. longipes* was of interest to test whether evidence suggested the endemic evolved from sympatric populations on the sand dunes or from populations presently found away from the sand dunes. Finally, we wanted to contribute to the growing body of knowledge concerning genetic diversity in rare species.

MATERIALS AND METHODS

Population sampling. The locations of the populations that were sampled for this study can be found in FIGURE 2.1 and TABLE 2.1.The numbers of populations and individuals, respectively, examined for each species were: *Stellaria arenicola* (14, 302), *S. longipes* -dunes (3, 58), and *S. longipes* -other (4, 83). Populations of the endemic *S. arenicola* were sampled throughout the range of the species. Populations of the related progenitor *S. longipes* were collected from the borders of the dune fields and in other habitats in Alberta and Saskatchewan (FIGURE 2.1). Voucher specimens were deposited in the herbarium at the University of Alberta (ALTA). Seeds were collected from up to 50 individuals in each population. In addition, we collected progeny arrays that consisted of at least 30 seeds from each of 24 hermaphroditic individuals in two populations of each species. The collections were transported to the phytotron at the University of Alberta, where the seeds were germinated and seedlings grown in soil. For the population collections, one progeny per parent was used in the electrophoretic analysis. For the progeny arrays, up to 24 progeny per mother plant were used.

Electrophoresis. Standard methods for starch gel electrophoresis were employed in this study (Soltis et al., 1983). Fresh pieces of actively growing leaf tissue were ground in cold Tris-HCl extraction buffer: 0.1 M Tris-HCl, pH 7.5, 4.0 mM 2-mercaptoethanol, 1.0 mM EDTA (disodium salt), 0.2 M sucrose, 0.6% polyvinyl-poly-pyrrolidone (5:1 ratio of 40K:360K m.w.), 2% PEG (8 K m.w.), 0.1% BSA, and 2.0 mM ascorbic acid. The supernatant was absorbed onto filter paper wicks, frozen at -20° C overnight, and electrophoresed the following morning. The filter paper wicks were loaded onto 12% starch gels.

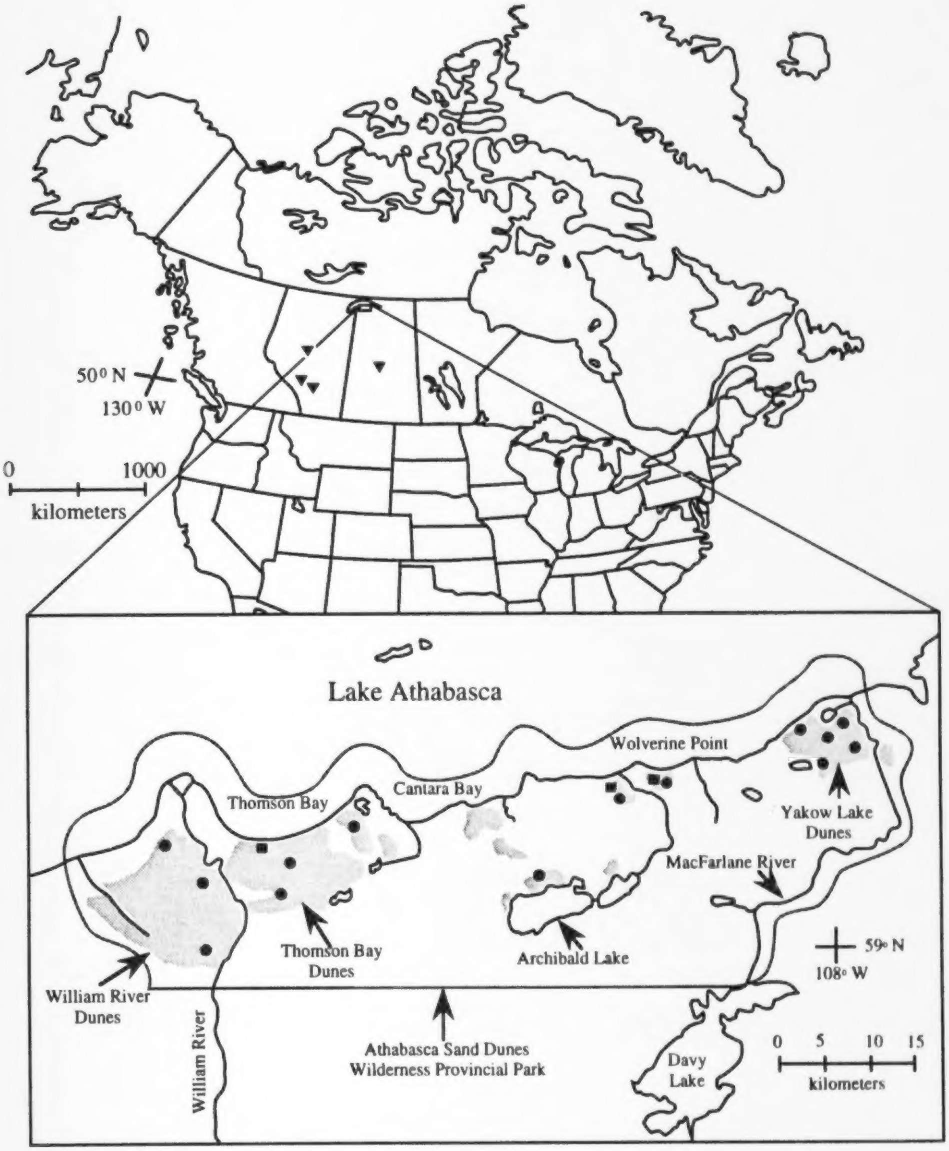

FIGURE 2.1. Location of populations sampled in this study of the widespread *Stellaria longipes* (triangles [western North America], squares [Athabasca sand dunes]) and the endemic *S. arenicola* (circles) from the Athabasca sand dunes.

Three systems were used to resolve the isozymes in this study. System I: gel buffer of one part 0.038 M $LiOH \cdot H_2O$ - 0.188 M boric acid (pH 8.3), and nine parts 0.045 M Tris - 7.0 mM citric acid (pH 8.4) (Soltis et al., 1983); electrode buffer containing only the lithium-borate constituent. System II: electrode buffer of 0.4 M citric acid$\cdot H_2O$ (trisodium salt), 1.0 M HCl to pH 7.0; gel buffer of 0.02 M L-histidine$\cdot$HCl monohydrate, 1.0 M NaOH to pH 7.0 (Soltis et al., 1983). System III: electrode buffer of 0.065 M L-histidine (free base) - 0.065 M citric acid$\cdot H_2O$ (pH 6.5); gel buffer containing electrode buffer and distilled water in a 1:3 ratio, respectively (Cardy, Stuber and Goodman, 1983). System I was run at 50 mA for 30 min, then at 60mA for 4-5 hr. System II was run at 100 mA for 30 min, then at 110 mA for 4-5 hr. System III was run at 30 mA for 4-5 hr. The electrophoresis was performed at 4° C.

Fifteen enzyme systems were resolved in this study. Leucine aminopeptidase (LAP), phosphoglucose isomerase (PGI), glutamate oxalate-transferase (GOT), aldolase (ALDO), aconitase (ACO), alcohol dehydrogenase (ADH), and glutamate dehydrogenase (GDH) were resolved on system I. Malate dehydrogenase ([NAD]MDH), 6-phosphogluconate (PGD), phosphoglucose mutase (PGM), and malate dehydrogenase ((NADP)ME) were resolved on system II. Menadione reductase (MNR), isocitrate dehydrogenase (IDH), shikimic acid dehydrogenase (SKD), and glyceraldehyde-3-phosphate dehydrogenase (G3PDH) were resolved on system III. PGD, G3PDH, MDH, MNR, and PGM were used to assess outcrossing rates in the progeny array analysis.

Enzymatic assays followed Soltis et al. (1983), except for MNR and ADH (Wendel and Weeden, 1989). The locus specifying the most anodally migrating isozyme was designated as 1, the next 2, and so on. Similarly, the most anodal allozyme of a gene was labeled A, etc. Isozymes and allozymes were inferred by observing segregation of bands among individuals in the populations sampled, from segregation patterns in the open-pollinated progeny arrays, and from previous studies on the species (Cai and Chinnappa, 1989a, 1989b; Cai, Macdonald, and Chinnappa, 1990). All populations were determined to be tetraploid ($2n$=52) using the fuelgen staining method (Bayer, 1992) on root tips. The isozyme banding patterns conformed to those expected for tetrasomic inheritance. Homozygotes were scored as having four copies of the allele, balanced heterozygotes as having two copies of each allele, unbalanced heterozygotes as having one and three copies of the respective alleles. Banding intensity was used to identify unbalanced heterozygotes. Allozyme frequencies at each locus were determined for each population; genotype frequencies were determined at each locus for the progeny arrays.

TABLE 2.1. Population designation, collection location, and habitat for 14 populations of the endemic *Stellaria arenicola* and seven populations of the widespread *S. longipes* used in this study.

Pop.	Population location and habitat.
	S. arenicola
wrd1	North William River dune field. Lat. 59^{0} 05’ N., Long. 109^{0} 20’ W., elev. 230 m. Active sand dunes.
wrd2	Central William River dune field. Lat. 59^{0} 03’N., Long. 109^{0} 15’ W., elev. 244 m. Gravel plains.
wrd3	South William River dune field. Lat. 58^{0} 55’ N., Long. 109^{0} 12’ W., elev. 275 m. Active sand dunes.
tbd1	Central Thomson Bay dune field. Lat. 59^{0} 03’ N., Long. 109^{0} 05’ W., elev. 270 m. Active sand dunes.
tbd2	South Thomson Bay dune field. Lat. 59^{0} 00’ N., Long. 109^{0} 08’ W., elev. 270 m. Active sand dunes.
tbd3	Cantara Lake dune field. Lat. 59^{0} 06’ N., Long. 108^{0} 49’ W., elev. 230 m. Active sand dunes.
cad1	West Wolverine dune field. Lat. 59^{0} 08’ N., Long. 108 ^{0} 25’ W., elev. 245 m. Active sand dunes.
cad2	East Wolverine dune field. Lat. 59^{0} 07’ N., Long. 108^{0} 20’ W., elev. 245 m. Active sand dunes.
yld1	Eastern Yakow Lake dune field. Lat. 59^{0} 12’ N., Long. 107^{0} 55’ W, elev. 245 m. Active sand dunes.
yld2	Eastern Yakow Lake dune field. Lat. 59^{0} 10’ N., Long. 107^{0} 55’ W, elev. 255 m. Active sand dunes.
yld3	Central Yakow Lake dune field. Lat. 59^{0} 10’N., Long. 108^{0} 00’ W., elev. 240. Active sand dunes.
yld4	South Yakow Lake dune filed. Lat. 59^{0} 09’ N., Long. 108^{0} 05’ W., elev. 250 m. Active sand dunes.
yld5	Northwest Yakow Lake dune field. Lat. 59^{0} 11’ N., Long. 108^{0} 10’ W., elev. 220 m. Active sand dunes.
cad3	Archibald Lake dune field. Lat. 59^{0} 02’ N., Long. 108^{0} 35’ W., elev. 305 m. Active sand dunes.
	S. longipes
dun1	West Wolverine Point shoreline. Lat. 59^{0} 07’ N., Long. 108^{0} 25’ W., elev. 215 m. Moist beach habitat.
dun2	East Wolverine Point shoreline. Lat. 59^{0} 07’ N., Long. 108^{0} 20’ W., elev. 215 m. Moist beach habitat.
dun3	Thomson Bay shoreline. Lat. 59^{0} 05’ N., Long. 109^{0} 10’ W., elev. 215 m. Moist beach habitat.
lon1	Ram Mountain, Alberta. Lat. 52^{0} 20’ N, Long. 115^{0} 45’ W, elev. 1,860 m. Open subalpine forest.
lon2	East shore of Lesser Slave Lake, Alberta. Lat. 55^{0} 20’ N., Long. 114^{0} 45’ W., elev. 605 m. Beach habitat.
lon3	Gem Lake, Sask. Lat. 54^{0} 03 ‘N., Long. 104^{0} 40’ W., elev. 557 m. Moist meadow in jack pine forest.
lon4	Nose Hill, Alberta. Lat. 51^{0} 08’ N., Long. 114^{0} 10’ W., elev. 1285 m. Moist prairie.

Genetic analysis. To estimate the extent of genetic variation within populations, the following statistics were computed: A, the mean number of alleles per locus; A_P, the mean number of alleles per polymorphic loci; P, the proportion of polymorphic loci when the most common allele has a frequency less than 0.95; and H_E, the expected panmictic heterozygosity. T-tests were used to test for significant differences among these population parameters. The partitioning of genetic diversity within and among populations was analyzed using measures proposed by Nei (1973). Genetic identities (Nei, 1972) were calculated as well. Population variation statistics (A, A_P, P, H_E) and standard genetic identities were calculated using the BIOSYS program (Swofford and Selander, 1989). Genetic diversity statistics were calculated using the GENESTAT-PC program (Whitkus, 1988). Principal components analysis (PCA) using the NT-SYS-pc program (Rohlf, 1987) helped evaluate the phenetic interpopulational relationships based on allele frequency distributions, with only polymorphic loci included in the analysis.

Outcrossing rates were determined using the multilocus outcrossing estimation program for tetraploids, TETRAT (Ritland, 1990). The single and multilocus outcrossing rates represent the proportion of progeny that are the result of outcrossing, 1.00 being the maximum value. TETRAT incorporates tetrasomic inheritance and can estimate four-gene fixation indices (Ritland, 1990). It determines the statistical variance of estimates by the bootstrap method. We performed 99 bootstraps per population.

RESULTS

The 15 enzyme systems assayed in this study are coded by 27 putative loci. Some isozymes were excluded from our analysis because they were poorly resolved on our systems or have complex banding patterns (GOT-2, PGI-2, PGI-3, PGM-3). Eleven of the loci were monomorphic in all populations: *Aco-1*, *Aldo-1*, *Aldo-2*, *Got-1*, *Idh-2*, *Lap-1*, *Lap-2*, *Me-1*, *Pgi-1*, *Pgm-1*, and *Skd-2*. Sixteen loci, *Pgd-1*, *Pgd-2*, *Aco-2*, *Adh-1*, *G3pdh-1*, *Gdh-1*, *Got-2*, *Idh-1*, *Mdh-1*, *Mdh-2*, *Mdh-3*, *Mnr-2*, *Mnr-3*, *Pgm-1*, *Pgm-2*, and *Skd-1*, were polymorphic in at least some populations (TABLE 2.2).

TABLE 2.2. Allele frequency data for polymorphic loci from 14 populations of the endemic *Stellaria arenicola* and seven populations of the wdespread *S. longipes*. * indicates alleles unique to *S. arenicola*, ** indicates alleles restricted to the sand dunes, and *** indicates alleles not found on the sand dunes.

Locus/	*S. arenicola*													
allele	wrd1	wrd2	wrd3	tbd1	tbd2	tbd3	cad1	cad2	yld1	yld2	yld3	yld4	yld5	cad3
Pgd-1														
a**	-	-	-	-	-	-	-	-	-	-	-	-	0.08	0.03
b	0.84	0.86	0.85	1.00	1.00	0.94	0.70	0.83	0.94	0.94	0.89	0.92	0.90	0.85
c	0.16	0.14	0.15	-	-	0.06	0.30	0.17	0.06	0.06	0.11	0.08	0.03	0.10
d*	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03
Pgd-2														
a***	-	-	-	-	-	-	-	-	-	-	-	-	-	-
b	0.81	0.39	0.80	0.67	0.45	0.70	0.80	0.60	0.56	0.56	0.53	0.56	0.30	0.38
c	0.19	0.39	0.20	0.25	0.35	0.30	0.20	0.27	0.40	0.11	0.19	0.33	0.45	0.63
d	-	0.22	-	0.08	0.20	-	-	0.13	0.04	0.33	0.28	0.11	0.25	-
e***	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aco-2														
a***	-	-	-	-	-	-	-	-	-	-	-	-	-	-
b	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
c***	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Adh-1														
a**	-	0.03	-	-	-	-	-	-	-	-	-	-	-	-
b	0.13	0.08	-	0.14	0.08	-	0.05	-	0.10	-	-	-	0.03	0.08
c	0.88	0.89	1.00	0.86	0.93	1.00	0.95	1.00	0.90	1.00	1.00	1.00	0.98	0.93
G3pdh-1														
a**	0.20	-	-	-	-	-	-	-	0.04	0.08	-	0.17	0.08	-
b	0.80	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.96	0.92	1.00	0.83	0.93	1.00

Gdh-1														
a	1.00	1.00	0.95	1.00	1.00	1.00	0.90	1.00	1.00	1.00	1.00	1.00	0.98	0.88
*b***	-	-	0.05	-	-	-	0.10	-	-	-	-	-	0.03	0.13
Got-2														
*a****	-	-	-	-	-	-	-	-	-	-	-	-	-	-
b	-	-	0.05	-	-	-	-	-	-	0.06	0.06	0.06	0.05	-
c	1.00	1.00	0.95	1.00	1.00	1.00	1.00	1.00	1.00	0.94	0.94	0.94	0.95	1.00
Idh-1														
a	0.98	0.94	1.00	0.94	0.98	0.92	1.00	1.00	0.90	0.86	0.81	0.86	0.93	0.95
b	0.02	0.06	-	0.06	0.03	0.08	-	-	0.10	0.14	0.19	0.14	0.08	0.05
Mdh-1														
*a***	-	0.06	-	-	-	-	0.13	0.04	-	-	0.03	0.03	0.23	-
b	1.00	0.94	1.00	1.00	1.00	1.00	0.68	0.90	0.94	0.97	0.97	0.97	0.55	1.00
c	-	-	-	-	-	-	0.20	0.06	0.06	0.03	-	-	0.23	-
*d****	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mdh-2														
a	-	-	-	-	-	-	-	-	-	-	-	-	-	-
b	0.89	0.83	1.00	1.00	0.93	0.94	1.00	1.00	0.94	0.94	0.81	0.94	1.00	1.00
c	-	0.17	-	-	0.08	-	-	-	0.06	0.06	0.19	0.06	-	-
*d***	0.11	-	-	-	-	0.06	-	-	-	-	-	-	-	-
Mdh-3														
*a***	-	-	0.05	-	-	0.27	-	0.02	0.04	-	-	-	0.03	0.03
*b****	-	-	-	-	-	-	-	-	-	-	-	-	-	-
c	1.00	1.00	0.95	0.97	1.00	0.73	1.00	0.98	0.96	1.00	1.00	1.00	0.98	0.98
d	-	-	-	0.03	-	-	-	-	-	-	-	-	-	-
Mnr-2														
a	-	0.36	0.28	0.39	0.23	0.03	0.13	0.08	0.19	0.31	0.28	0.17	-	-
b	0.06	-	-	-	-	0.06	-	-	-	-	-	-	0.08	-
c	0.94	0.64	0.73	0.61	0.75	0.91	0.85	0.69	0.81	0.69	0.67	0.78	0.93	1.00
d	-	-	-	-	0.03	-	0.03	0.13	-	-	0.06	0.06	-	-
e	-	-	-	-	-	-	-	0.10	-	-	-	-	-	-
Mnr-3														
a	-	-	-	0.06	-	-	-	-	0.02	-	-	-	-	-
b	1.00	0.94	1.00	0.94	1.00	1.00	1.00	1.00	0.96	0.86	1.00	0.92	1.00	1.00
c	-	0.06	-	-	-	-	-	-	0.02	0.14	-	0.08	-	-
Pgm-1														
a	0.98	0.75	1.00	0.83	0.50	0.70	0.93	0.94	0.81	1.00	0.83	0.69	0.60	0.88
*b***	0.02	0.25	-	0.17	0.50	0.30	0.08	0.06	0.19	-	0.17	0.31	0.40	0.13
Pgm-2														
*a***	-	-	-	-	-	-	0.23	0.33	-	-	-	-	-	-
b	0.98	0.67	0.95	0.92	0.85	1.00	0.78	0.67	0.96	1.00	1.00	0.86	0.93	0.78
c	0.02	0.33	0.05	0.08	0.15	-	-	-	0.04	-	-	0.14	0.08	0.23
Skd-1														
*a***	0.08	-	-	0.25	0.13	0.47	-	0.04	0.13	-	-	-	-	0.38
b	0.92	1.00	1.00	0.69	0.88	0.53	1.00	0.77	0.88	1.00	1.00	1.00	1.00	0.63
c	-	-	-	0.06	-	-	-	0.19	-	-	-	-	-	-

TABLE 2.2. continued.

Locus/ allele	*S. longipes*						
	dun1	dun2	dun3	lon1	lon2	lon3	lon4
Pgd-1							
*a***	-	-	0.06	-	-	-	-
b	0.90	0.85	0.92	0.89	0.89	0.89	0.74
c	0.10	0.15	0.03	0.11	0.12	0.11	0.26
*d**	-	-	-	-	-	-	-
Pgd-2							
*a****	-	-	-	0.11	-	-	-
b	0.28	0.35	0.44	0.11	0.54	0.50	0.14
c	0.45	0.40	0.28	0.33	0.31	0.50	0.43
d	0.28	0.25	0.28	0.44	0.15	-	0.21

e***	-	-	-	-	-	-	0.21
Aco-2							
a***	-	-	-	0.28	-	-	-
b	1.00	1.00	1.00	0.72	0.92	1.00	1.00
c***	-	-	-	-	0.08	-	-
Adh-1							
a**	-	-	0.06	-	-	-	-
b	0.03	-	0.08	0.14	0.17	0.14	0.07
c	0.98	1.00	0.86	0.86	0.83	0.86	0.93
G3pdh-1							
a**	-	-	0.17	-	-	-	-
b	1.00	1.00	0.83	1.00	1.00	1.00	1.00
Gdh-1							
a	0.90	0.90	0.86	1.00	1.00	1.00	1.00
b**	0.10	0.10	0.14	-	-	-	-
Got-2							
a***	-	-	-	0.17	-	-	-
b	-	0.05	-	-	0.54	0.89	0.86
c	1.00	0.95	1.00	0.83	0.46	0.11	0.14
Idh-1							
a	1.00	1.00	0.94	1.00	0.92	1.00	1.00
b	-	-	0.06	-	0.08	-	-
Mdh-1							
a**	0.13	-	-	-	-	-	-
b	0.75	0.90	0.92	1.00	0.71	0.86	1.00
c	0.13	0.10	0.08	-	0.29	0.08	-
d***	-	-	-	-	-	0.06	-
Mdh-2							
a	-	-	0.11	-	-	-	-
b	1.00	0.88	0.78	1.00	0.92	1.00	1.00
c	-	0.03	0.06	-	0.08	-	-
d**	-	0.10	0.06	-	-	-	-
Mdh-3							
a**	0.05	-	-	-	-	-	-
b***	-	-	-	0.14	-	-	-
c	0.95	0.83	1.00	0.86	1.00	0.86	1.00
d	-	0.18	-	-	-	0.14	-
Mnr-2							
a	0.10	0.15	0.17	0.06	-	-	0.07
b	-	0.05	-	0.28	-	-	-
c	0.90	0.80	0.78	0.64	0.73	0.89	0.50
d	-	-	0.06	-	0.12	0.05	0.07
e	-	-	-	0.03	0.15	0.06	0.36
Mnr-3							
a	0.08	0.10	-	0.03	-	-	-
b	0.93	0.90	0.92	0.97	1.00	1.00	0.98
c	-	-	0.08	-	-	-	0.02
Pgm-1							
a	0.60	0.55	0.81	1.00	1.00	1.00	1.00
b**	0.40	0.45	0.19	-	-	-	-
Pgm-2							
a**	-	0.08	-	-	-	-	-
b	1.00	0.70	1.00	0.83	1.00	0.89	0.57
c	-	0.23	-	0.17	-	0.11	0.43
Skd-1							
a**	0.05	-	-	-	-	-	-
b	0.95	1.00	1.00	1.00	0.77	0.89	1.00
c	-	-	-	-	0.23	0.11	-

Fifty-two alleles were detected at the 16 polymorphic loci (TABLE 2.2). Thirty-one of these alleles were found in populations of the endemic species, and populations of the progenitor species located both on the Athabasca sand dunes and away from the sand dunes. Ten alleles were restricted to sand dune populations of both the endemic and progenitor species (*Pgm-1b, Pgm-2a, Adh-1a, Skd-1a, Pgd-1a, Mdh-1a, Mdh-2d, Mdh-3a, G3pdh-1a, and Gdh-1b*). One allele was unique to the endemic species (*Pgd-1d*) and one allele was unique to dune populations of the progenitor (*Mdh-2a*). Seven alleles were restricted to populations of the progenitor species located away from the sand dunes *(Pgd-2a, Pgd-2e, Got-2a, Mdh-1d, Mdh-3b, Aco-2a* and *Aco-2c*). In addition, two alleles were found in populations of the endemic species and in the progenitor species located away from the sand dunes, but were not found in populations of the progenitor on the Athabasca sand dunes (*Mnr-2e* and *Skd-1c*). Most of the alleles having a restricted distribution occur in low frequency or in few populations. Only two loci (*Got-2* and *Pgd-2*) differed among groups for the most common allele.

The mean number of alleles per locus (A) ranged from 1.25 to 1.63 with a mean of 1.41 for the endemic populations and 1.48 for the progenitor populations (TABLE 2.3). The mean number of alleles per polymorphic locus (A_P) ranged from 2.00 to 2.62. The endemic populations had a mean A_P of 2.23, and the progenitor populations had a mean A_P of 2.36. Values of P, the percent polymorphic loci, ranged from 22.2 to 40.7 with a mean of 29.9 in the endemic and 33.8 in the progenitor populations. The expected panmictic heterozygosity (H_E) ranged from 0.051 to 0.127 with a mean of 0.087 in the endemic and 0.107 in the progenitor populations. A_P, P, and H_E were significantly less ($P < 0.05$) in the endemic populations than populations of the progenitor taxon.

TABLE 2.3. Summary of allozyme variation for 27 loci within 14 populations of the endemic *Stellaria arenicola* and seven populations of the widespread *S. longipes*. A locus was considered polymorphic if the most common allele frequency was less than 0.95[1]

Population	N	A	A_P	P	H_E
	S. arenicola				
wrd1	32	1.37	2.00	25.9	0.06
wrd2	18	1.44	2.20	37.0	0.11
wrd3	20	1.25	2.00	25.9	0.05
tbd1	20	1.37	2.25	29.6	0.09
tbd2	18	1.37	2.22	25.9	0.09
tbd3	32	1.33	2.12	29.6	0.09
cad1	20	1.44	2.50	29.6	0.09
cad2	24	1.48	2.62	25.9	0.09
yld1	24	1.55	2.15	33.3	0.09

yld2	18	1.37	2.25	29.6	0.09
yld3	18	1.37	2.25	25.9	0.08
yld4	18	1.48	2.18	37.0	0.10
yld5	20	1.55	2.25	33.3	0.10
cad3	20	1.41	2.22	29.6	0.09
S. longipes					
dun1	20	1.44	2.20	33.3	0.09
dun2	18	1.63	2.55	40.7	0.12
dun3	20	1.56	2.36	40.7	0.13
lon1	18	1.48	2.44	29.6	0.11
lon2	26	1.44	2.20	37.0	0.12
lon3	18	1.37	2.22	33.3	0.08
lon4	21	1.41	2.57	22.2	0.10
Mean of *S. arenicola*	21.6	1.41	2.23*	29.9*	0.087*
(SE)	1.3	0.02	0.04	1.1	0.00
Mean of *S. longipes*	20.1	1.48	2.36*	33.8*	0.107*
(SE)	1.1	0.03	0.06	2.5	0.01

[1] sample size (N), mean number of alleles per locus (A), mean number of alleles per polymorphic locus (A_P), percent polymorphic loci (P), mean expected heterozygosity (H_E). * indicates $P < 0.05$.

Gene diversity statistics were calculated and then averaged over all loci (TABLE 2.4). The progenitor populations away from the sand dunes had the highest total genetic diversity($H_T = 0.212$), the progenitor populations from the dunes had somewhat lower levels of genetic diversity (0.197), and the endemic populations had the lowest mean values of H_T (0.163). The progenitor populations located away from the sand dunes had the highest level of population differentiation($G_{ST} = 0.183$), whereas the progenitor populations from the sand dunes had the lowest level of population differentiation (0.041). The endemic populations had a mean G_{ST} value of 0.102, intermediate to that of the other groups.

TABLE 2.4. Genetic diversity statistics (Nei, 1973) for *Stellaria arenicola* and two groups of *S. longipes*. Values presented are means over all polymorphic loci.[1]

Taxa	H_T	H_S	G_{ST}
S. arenicola	0.163	0.147	0.102
S. longipes -dunes	0.197	0.189	0.041
S. longipes -other	0.212	0.173	0.183

[1] H_T = total gene diversity; H_S = gene diversity within populations; and G_{ST} = the proportion of total gene diversity found among populations.

Intraspecific and interspecific genetic identities averaged for the three groups are presented in TABLE 2.5. The populations were all closely related with the range of identities from 0.932 to 1.000. The endemic populations were more closely related to the progenitor populations from the sand dunes than those away from the sand dunes. Likewise, *Stellaria longipes* populations from the sand dunes were more closely related to the sympatric *S. arenicola* populations than the allopatric populations of *S. longipes*. Populations of the progenitor located away from the sand dunes had the same mean identity with both progenitor and endemic populations from the sand dunes. Based on a PCA of allele frequency data, all sand dune populations were closely related regardless of the taxon, whereas the progenitor populations from non-sand dune habitats are grouped away from the sand dune populations (FIGURE 2.2).

TABLE 2.5. Matrix of gene identities (Nei, 1972) averaged over populations of *Stellaria arenicola* and *S. longipes* from the sand dunes and from other habitats. Ranges are given in brackets.

Species	N	*S. arenicola*	*S. longipes* - dunes	*S. longipes* - other
S. arenicola	14	0.989 (0.977 - 0.999)		
S. longipes - dunes	3	0.990 (0.980 - 1.000)	0.995 (0.992 - 0.997)	
S. longipes - other	4	0.959 (0.932 - 0.982)	0.959 (0.947 - 0.980)	0.983 (0.976 - 0.991)

The endemic, *S. arenicola*, had a lower outcrossing rate ($P < 0.05$) than *S. longipes* populations from the sand dunes (TABLE 2.6). Single locus outcrossing rates differed between the two taxa and from multilocus outcrossing rates within taxa (TABLE 2.6). When single locus estimates of outcrossing are lower than multilocus estimates, biparental inbreeding (outcrossing between relatives) may be occurring (Shaw, Kahler, and Allard, 1981). The two-, three-, and four-gene fixation indices were positive, indicating that the plants practice some selfing. The lower three- and four-gene fixation indices indicate that localized mating is causing some level of biparental inbreeding to occur in these populations.

TABLE 2.6. Estimates of outcrossing rates and gene fixation indices for *Stellaria arenicola* and *S. longipes* from the Athabasca sand dunes. Standard errors are enclosed in brackets.

	Taxa^{1}	
Parameter	*S. arenicola*	*S. longipes*
Outcrossing rate		
Multilocus outcrossing rate	0.667 (0.046)a	0.802 (0.048)b
Single locus outcrossing rate	0.523 (0.043)a	0.714 (0.060)b
Difference	0.145 (0.021)*	0.088 (0.025)
Fixation indices		
Two-gene fixation index	0.201 (0.023)	0.167 (0.017)
Variance of two-gene fixation index	0.106 (0.012)	0.077 (0.011)
Three-gene fixation index	0.085 (0.016)	0.072 (0.015)
Four-gene fixation index	0.072 (0.015)	0.059 (0.014)
No. of families	40	34
No. of progeny over all families	791	635

[1] lowercase letters indicate values differ between species ($P < 0.05$). * indicates single and multilocus outcrossing rates differ ($P < 0.05$).

DISCUSSION

Amount and pattern of genetic variation. Although Stebbins (1942) suggested long ago that endemic taxa were genetically depauperate, it wasn't until techniques became available to reveal protein and DNA variation that this statement could be extensively tested. Information on the population biology and genetics of endemic, regional, and widespread species has increased in recent years. In a recent summary of allozyme variation in plant species, Hamrick and Godt (1989) found that the geographic range of a species accounted for the largest amount of genetic variation in population and species level statistics. Species with small ranges typically have less genetic variation than regional or widespread taxa (Gottlieb, 1973; Karron et al., 1988; Loveless and Hamrick, 1988; Pleasants and Wendel, 1989; Bayer, 1992).

Our isozyme data indicated that *Stellaria arenicola* has lower genetic variation at the population level than *S. longipes*. This was demonstrated in the mean number of alleles per polymorphic locus, percent polymorphic loci, and panmictic heterozygosity. Other studies of recently evolved sympatric species have found the derivative to be depauperate in genetic variation (Gottlieb, 1973, 1974), although not always (Gottlieb and Pilz, 1976). Strong directional selection, or changes in allele frequencies due to chance (drift, founder effects), are factors thought responsible for the reduction in genetic variation in endemic species (Karron, 1987). Inbreeding and founder effects were responsible for the reduced genetic variation in *Stephanomeria malheurensis*, a recently evolved sympatric species endemic to one mountain in Oregon (Gottlieb, 1973). Macdonald et al. (1987) previously suggested that strong selection for sand dune-adapted traits was responsible for the evolution of the endemic *S. arenicola*.

Populations of *Stellaria longipes* were found to have higher total genetic diversity, and higher within population genetic diversity than the endemic *S. arenicola* (TABLE 2.4), similar to the pattern found in other studies (Hamrick and Godt, 1989). Population differentiation is most affected by the breeding system of the organism under study (Hamrick and Godt, 1989) and not by the geographic range of the species. The higher population differentiation of the progenitor *S. longipes* is likely due to the more extensive geographic distribution of the populations collected for this study and the greater interpopulational distances characteristic of the progenitor. The three *S. longipes* populations from the sand dunes show very low population differentiation compared to the endemic *S. arenicola*, although both were collected over a similar range. Higher population differentiation in the endemic would be expected if populations were isolated and small; however, the endemic is quite abundant within its limited range. Other factors that might reduce gene flow among populations of the endemic, such as a shift in breeding system, could account for the higher population differentiation observed.

Breeding systems. Previous studies suggested a shift to inbreeding, from primarily outcrossing, contributed to the evolution of the endemic *Stellaria arenicola* (Chinnappa and Morton, 1984). Macdonald et al. (1987) found reduced protandry in populations of the endemic and progenitor *Stellaria* species on the sand dunes as well as a slight shift to earlier flowering in the endemic. A major shift in breeding system to selfing from obligately outcrossing was responsible for the evolution of at least one other sympatric species pair (Gottlieb, 1973). Variation among individuals in the proportions of offspring produced by selfing, or outcrossing, has been studied in relatively few instances (Brown, Burdon, and Jarosz, 1989). Although it has been suggested that geographically restricted taxa exhibit greater self-compatibility and higher levels of inbreeding than closely related widespread congeners, the evidence accumulated to date is inconclusive (Karron, 1987, 1989).

Our electrophoretic analysis of progeny arrays revealed a significantly higher rate of selfing in *Stellaria arenicola* populations relative to *S. longipes* populations on the Athabasca sand dunes. In addition, evidence provided by comparisons of the single and multilocus outcrossing rates and the relationships of the two-, three-, and four-gene fixation indices suggests that some of the selfing is due to biparental inbreeding, or outcrossing with relatives (Shaw, Kahler, and Allard, 1981; Bayer, Ritland, and Purdy, 1990). Although we found a significant difference in outcrossing rate between *S. arenicola* and *S. longipes*, breeding systems of the two species could still be considered to be relatively similar. Other studies have found even higher variation in outcrossing rates among populations of single species (Glover and Barrett, 1986; Holtsford and Ellstrand, 1989).

Morphological aspects and demography of the endemic on the sand dunes might be partly responsible for the lower outcrossing rates. *Stellaria arenicola* was found to have more flowers on individual ramets and to have significantly more of its ramets in reproductive mode than individuals of *S. longipes* (Macdonald et al., 1987). This might significantly affect pollinator foraging, resulting in higher geitonogamous pollination (crossing between flowers from the same genetic individual). In addition, established individuals of the endemic tend to stabilize the sand around them providing a good habitat for seed germination and seedling establishment (B. Purdy, personal observation). This results in large clumps of *S. arenicola* that appear as genets but are in fact a conglomeration of isozymically closely related individuals (B. Purdy, unpublished data). A patchy distribution of clumps of *S. arenicola* results in pollinators foraging among many flowers within clumps before moving off to new patches. This would result in significant within-family outcrossing, responsible for the observed functional inbreeding. Higher inbreeding may have been instrumental in the rapid evolution of the endemic *S. arenicola* by allowing fixation of adaptive gene complexes and by reducing gene flow with sympatric populations of the progenitor *S. longipes.*

Origin of Stellaria arenicola. It has been predicted that recently derived species exhibit: 1) high genetic similarity with the progenitor taxon; 2) less genetic variation than the progenitor; 3) a subset of the allelic diversity found in the progenitor; and 4) few, if any, unique alleles, due to inadequate time for new mutations to accumulate (Gottlieb, 1973). Predictions concerning the allelic relationships of recently derived species with their progenitor species have been supported by a number of studies (Gottlieb, 1973, 1974; Crawford and Smith, 1982a, 1982b; Crawford, Ornduff, and Vasey, 1985; Gottlieb, Warwick, and Ford, 1985; Loveless and Hamrick, 1988; Pleasants and Wendel, 1989). All of these predictions are supported by the present study.

The mean genetic identity between pairs of *S. arenicola* populations was the same as that between populations of the endemic and sand dune populations of *S. longipes*. In fact, genetic identities indicated that populations of *S. longipes* from the sand dunes were more similar to populations of the endemic species than they were to *S. longipes* populations located away from the sand dunes.

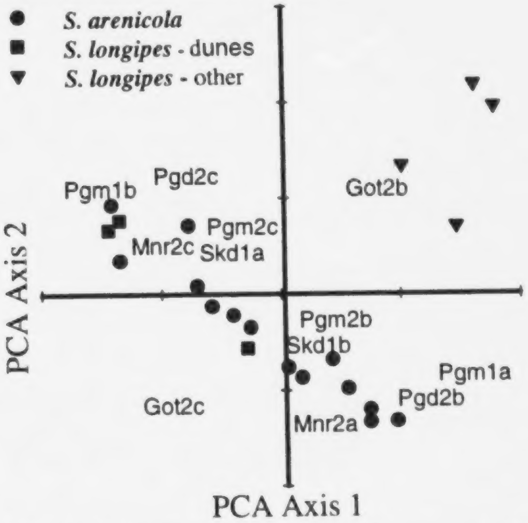

FIGURE 2.2. Principal components analysis of allele frequencies from populations of the endemic *Stellaria arenicola* and the widespread *S. longipes*. The first two principal components explain 26 and 24 % of the total variance respectively. Positions for OTUs (populations) and variables (alleles) are presented.

As predicted, the endemic *Stellaria arenicola* contained less genetic variation than *S. longipes*. The level of genetic variation in species of recent origin is a function of the genetic variation in the ancestral populations and the variation represented in the founding individuals. At all polymorphic loci except *Got-2* and *Pgd-2*, the endemic and progenitor populations shared the same most common allele. The data on patterns of allelic diversity and on genetic identity among populations strongly suggests the endemic *S. arenicola* is derived from the sympatric gene pool of the progenitor *S. longipes* that occurs presently on the Athabasca sand dunes. Further, the high identities suggest a recent origin for the endemic, and/or continued gene flow among derivative-progenitor populations, and is similar to other recent progenitor-derivative pairs where morphological divergence has occurred despite a lack of divergence at isozyme loci (Gottlieb, 1981; Crawford, 1983; Gottlieb, Warwick, and Ford, 1985; Loveless and Hamrick, 1988).

The sympatric evolution of the endemic *S. arenicola* has probably resulted in higher population genetic variation than would occur had the sand dune endemic evolved allopatrically because gene flow can still occur between the two species as they are reproductively compatible (Chinnappa and Morton, 1984) and co-occur in a number of areas on the sand dunes (Macdonald et al., 1987).

The flora of the Athabasca sand dunes represents one of the world's few boreal groups of endemic plants (Raup and Argus, 1982), a region known for its paucity of endemic species (Kruckeberg and Rabinowitz, 1985). Rapid speciation has occurred in other sand dune systems since the Pleistocene (Bowers, 1984; Pavlick, 1989). High rates of endemism in dune systems have been attributed to adaptation of plants to moving sand and barriers to dispersal and establishment (Bowers, 1984). The endemic taxa found on the Athabasca sand dunes occur both allopatric and sympatric to their progenitor species (Argus and Steele, 1979; Raup and Argus, 1982), and all but one have traits that could be considered adaptive for survival in a shifting sand dune environment. All of the endemic species are considered to have evolved after the sand dunes were formed at the end of the Pleistocene, 8,000 years ago (Raup and Argus, 1982).

Conservation. This study focused on the population genetic aspects of the sand dune endemic *Stellaria arenicola*, a species derived from the widespread *S. longipes*. Comparisons of the amount and pattern of genetic variation in this recently derived species with its progenitor were similar to other studies of similar species pairs and agreed with theoretical expectations. Despite the strong selection pressures on the sand dunes (Argus and Steele, 1979; Macdonald et al., 1987) and the inbreeding that is occurring in the endemic populations, *S. arenicola* still maintains relatively high genetic variation at the population level relative to populations of the widespread *S. longipes* from which it has evolved, and shows only moderate population differentiation.

One focus of a larger study was to investigate the population distribution and population genetics of the sand dune endemics to develop management plans for the vegetation of the Athabasca sand dunes, and because the endemic plants are candidates for the endangered species list in Canada. All populations of *S. arenicola* occur on isolated northern dune habitats not accessible by roads, and are protected by ecological reserve or wilderness provincial park status. The main threat to the populations of the endemic *S. arenicola* seen presently would be if gene flow with the progenitor were to increase to a level obscuring the morphological distinction of the endemic populations. Previous studies have shown, however, that strong selection pressure is keeping the progenitor genotypes from establishing on the harsher moving sand dune environment (Macdonald et al., 1987). Because there is little differentiation among populations of *S. arenicola* at isozyme loci, most of the gene pool for this restricted species can presently be captured in a few large populations. The largest populations also occur on the largest dune fields where the other sand dune endemics are most common. These are the areas where population monitoring should be focused in the future.

We are presently investigating the amount and pattern of genetic variation in other sand dune endemics to compare with the results found in this study. *Deschampsia mackenzieana* Raup, is an endemic grass found only on the Athabasca sand dunes that has evolved sympatrically with its widespread progenitor species *D. cespitosa* (L.) P. Beauv. *Salix silicicola* Raup and *Armeria maritima* (Mill.) Willd. subsp. *interior* (Raup) Pors. are two endemic taxa that are allopatric with progenitor populations of *Salix alaxensis* (Anderss.) Cov. and *Armeria maritima* subsp. *labradorica* (Wallr.) Hult., known to occur in more northerly locations. It will be of interest to observe the effect of sympatric and allopatric progenitor populations on the amounts and patterns of genetic variation found in the endemic plants from the Athabasca sand dunes.

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Chapter Three

Genetic diversity in the tetraploid sand dune endemic *Deschampsia mackenzieana* and its widespread diploid progenitor *D. cespitosa* (Poaceae) [1]

ABSTRACT. Electrophoretic variation was examined in 14 populations of tetraploid *Deschampsia mackenzieana*, an endemic of the Athabasca sand dunes in northern Saskatchewan, Canada, and 20 populations of its geographically widespread diploid progenitor, *Deschampsia cespitosa*. Three of the *Deschampsia cespitosa* populations were sympatric with the endemic on the Athabasca sand dunes. Populations of the endemic were found to have fewer alleles per locus (1.22 vs. 1.52), fewer alleles per polymorphic locus (2.17 vs. 2.70), lower percent polymorphic loci (18.9 vs. 30.5), and lower heterozygosity (0.062 vs. 0.119) than progenitor populations. Species level genetic diversity parameters also indicated that *Deschampsia mackenzieana* was genetically depauperate relative to its progenitor *Deschampsia cespitosa*. *Deschampsia mackenzieana* had no novel alleles but did share one allele with sympatric progenitor populations that did not occur in populations of *Deschampsia cespitosa* from other habitats. Although both species were found to partition most of their genetic diversity within populations, *Deschampsia mackenzieana* did have more of its limited genetic diversity partitioned among populations than *Deschampsia cespitosa*. The close genetic relationship between *Deschampsia mackenzieana* and sympatric populations of *Deschampsia cespitosa* may suggest the endemic tetraploid evolved from the sympatric diploid gene pool in the Athabasca sand dune region. The low levels of genetic diversity in *Deschampsia mackenzieana* suggest a restricted origin with limited gene flow from the progenitor since speciation.

INTRODUCTION

There is considerable variation in the amount and pattern of allozyme diversity in species of plants, much of it correlated with different life history strategies or breeding systems (Hamrick and Godt, 1989). Genetic diversity is an important aspect of a species' evolutionary potential (Holsinger and Gottlieb, 1991; Ellstrand and Elam, 1993), yet some studies have been unable to demonstrate a relationship between genetic diversity and the ecological breadth of a species (Babbel and Selander, 1974; Mashburn, Sharitz, and Smith, 1978; Levin, Ritter, and Ellstrand, 1979; Huenneke, 1991).

Polyploidy has the potential to increase the genetic variability, evolutionary potential, and perhaps the ecological amplitude of a species (Hunziker and Schaal, 1983). Despite the exploitation of polyploidy in agronomic species (improved yield, hybridization, etc.), there is still little understanding of its adaptive value in populations of wild species (Rothera and Davy, 1986). Polyploidy is prevalent in higher plants (Grant, 1981), but polyploid evolution has been rigorously investigated in relatively few instances (Stebbins, 1985; Bayer, 1987; Bayer, Purdy, and Lebedyk, 1991; Novak, Soltis, and Soltis, 1991; Thompson and Lumaret, 1992).

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[1] A version of this chapter has been published. Purdy and Bayer, 1995. *American Journal of Botany* **82**: 121-130.

Deschampsia mackenziana

Many isozyme studies of polyploid taxa have focused on determining the parentage of polyploids (Roose and Gottlieb, 1976; Bryan and Soltis, 1987; Rieseberg and Warner, 1987; Ashton and Abbott, 1992; Gastony, 1990) rather than the amount and pattern of genetic variation among closely related diploid and polyploid taxa (Soltis and Soltis, 1989). However, results from electrophoretic studies on *Tolmiea menziesii* (Soltis and Rieseberg, 1986; Soltis and Soltis, 1989), *Antennaria* species (Bayer, 1989), *Dactylis glomerata* (Lumaret and Barrientos, 1990), *Stellaria longipes* (Cai, Macdonald, and Chinnappa, 1990), and *Marshallia mohrii* (Watson, Elisens, and Estes, 1991) reveal that tetraploid taxa generally have higher numbers of alleles, polymorphic loci, and levels of heterozygosity than related diploid progenitor species.

Deschampsia mackenzieana Raup is an endemic grass of the Athabasca sand dunes in northwestern Saskatchewan, Canada (Raup, 1936; Raup and Argus, 1982). *Deschampsia mackenzieana* is related to the *D. cespitosa* (L.) P. Beauv. complex (Raup, 1936; Kawano, 1963). *Deschampsia cespitosa* is a geographically widespread species that is edaphically and morphologically variable (Kawano, 1963; Rothera and Davy, 1986). Tetraploid cytotypes of *D. cespitosa* have been recorded from Alaska (Kawano, 1963; Johnson and Packer, 1968) and Quebec (Hedberg, 1967) in North America as well as in Europe (Rothera and Davy, 1986). All other chromosome counts of *D. cespitosa* to the south and north of the Athabasca sand dunes have been diploid (Rothera and Davy, 1986). There are no previous reports on the cytology of *D. mackenzieana*.

This investigation was initiated to determine the amount and pattern of genetic variation in the sand dune endemic, *Deschampsia mackenzieana*, and its closely related, geographically widespread progenitor, *D. cespitosa*. We were interested in whether speciation affected the level of genetic diversity in the endemic *D. mackenzieana*. However, after determining the cytology of individuals of *D. mackenzieana* and *D. cespitosa*, the study became an investigation comparing populations of a diploid progenitor and tetraploid derivative species as well.

MATERIALS AND METHODS

Population sampling. The locations of the populations that were sampled for this study are found in FIGURE 3.1 and TABLE 3.1. Populations of *Deschampsia mackenzieana* were sampled throughout the range of the species, whereas populations of *D. cespitosa* were collected from the borders of the dune fields and from other habitats in western Canada and the United States (FIGURE 3.1). The number of populations and individuals, respectively, examined for each species were: *D. mackenzieana* (14, 416) and *D. cespitosa* (20, 617). The number of populations and individuals collected for *D. cespitosa* from different regions were: Athabasca sand dunes (3, 100), northern Rocky Mountains (4, 120), central Rocky Mountains and plains (9, 271), and southern Rockies (4, 126).

Live plants were collected from up to 50 individuals in each population. Seeds representing open-pollinated progeny arrays were collected from sand dune populations of *Deschampsia mackenzieana* and *D. cespitosa*. The collections were transported to the phytotron at the University of Alberta where the live plants and germinated seeds were grown in soil. Mitotic chromosome counts were made from squashed actively growing root tips using Feulgen stain (see Purdy, Bayer, and Macdonald, 1994 [chapter 2] for technique). All populations of *D. mackenzieana* were found to be tetraploid ($2n = 52$), whereas all populations of *D. cespitosa* were found to be diploid ($2n = 26$).

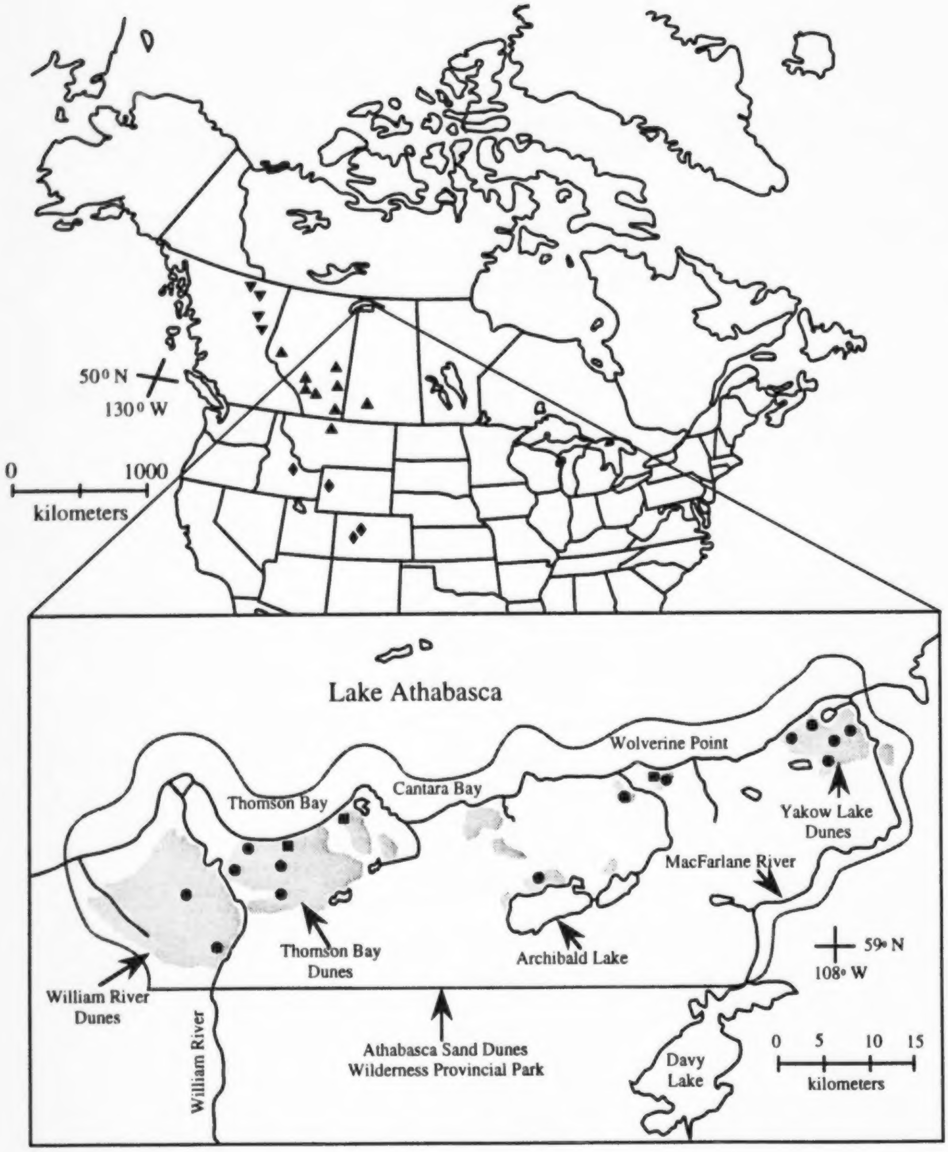

FIGURE 3.1. Locations of populations sampled in this study of the widespread *Deschampsia cespitosa* from the north (inverted triangle), central (triangle), south (diamond) and sand dune (squares) geographic regions, and the endemic *D. mackenzieana* (circles) from the Athabasca sand dunes.

***Electrophoresis*.** Standard methods for starch gel electrophoresis were employed in this study (Soltis et al., 1983; Purdy, Bayer, and Macdonald, 1994 [chapter 2]). Fresh pieces of actively growing leaf tissue were ground in cold extraction buffer. The supernatant was absorbed onto filter paper wicks, frozen at -20° C overnight, and electrophoresis was performed the following morning. The filter paper wicks were loaded onto 12% starch gels.

Three buffer systems were used to resolve the isozymes in this study. Thirteen enzyme systems were resolved. Leucine aminopeptidase (LAP), phosphoglucose isomerase (PGI), and glutamate oxalate-transferase (GOT) were resolved on system I (Purdy, Bayer, and Macdonald, 1994 [chapter 2]). Malate dehydrogenase ([NAD]MDH), menadione reductase (MNR), glyceraldehyde-3-phosphate dehydrogenase (G3PDH), glucose-6-phosphate dehydrogenase (G6PDH), and acid phosphatase (ACP) were resolved on system II. 6-phosphogluconate (6-PGD), isocitrate dehydrogenase (IDH), malate dehydrogenase ([NADP]ME), phosphoglucose mutase (PGM), and shikimic acid dehydrogenase (SKD) were resolved on system III.

Enzymatic assays followed those outlined in Purdy, Bayer, and Macdonald (1994 [chapter 2]). The locus specifying the most anodally migrating isozyme was designated as 1, the next 2, and so on. Similarly, the most anodal allozyme of a gene was labeled A, etc. Isozymes and allozymes were inferred by observing segregation of bands among individuals in the populations sampled, and from segregation patterns in open-pollinated progeny arrays. For tetraploid individuals, homozygotes were scored as having four copies of the allele, balanced heterozygotes as having two copies of each allele, unbalanced heterozygotes as having one and three copies of the respective alleles. Banding intensity was used to identify unbalanced heterozygotes. Allozyme frequencies at each locus were determined for each population.

TABLE 3.1. Population designation, collection location, habitat, and sample size for 14 populations of *Deschampsia mackenzieana* and 20 populations of *D. cespitosa* used in this study.

Pop.	Population location and habitat
	D. mackenzieana
wrd1	Central William River dune field. Lat. 59° 03' N., Long. 109° 20' W., elev. 244 m. Active sand
wrd2	South William River dune field. Lat. 58° 55' N., Long. 109° 12' W., elev. 275 m. Active sand
tbd1	West Thomson Bay dune field. Lat. 59° 05' N., Long. 109° 11' W., elev. 244 m. Active sand dunes.
tbd2	East Thomson Bay dune field. Lat. 59° 06' N., Long. 108° 59' W., elev. 270 m. Active rolling

tbd3	Central Thomson Bay dune field. Lat. 59° 03' N., Long. 109° 05' W., elev. 270 m. Active dunes.
tbd4	Thomson Bay shoreline. Lat. 59° 05' N., Lat. 109° 10' W., elev. 215 m. Disturbed beach ridges.
cad1	East Wolverine dune field. Lat. 59° 07' N., Long. 108° 20' W., elev. 245 m. Active sand dunes.
cad2	West Wolverine dune field. Lat. 59° 08' N., Long. 108° 25' W., elev. 245 m. Active sand dunes.
cad3	Archibald Lake dune field. Lat. 59° 02' N., Long. 108° 35' W., elev. 305 m. Active sand dunes.
yld1	Northwest Yakow Lake dune field. Lat. 59° 11' N., Long. 108° 10' W., elev. 220 m. Active sand
yld2	Northern Yakow Lake dune field. Lat. 59° 13' N., Long. 107° 59' W., elev. 220 m. Active sand
yld3	East Yakow Lake dune field. Lat. 59° 12' N., Long. 107° 55' W, elev. 245 m. Active sand dunes.
yld4	South Yakow Lake dune field. Lat. 59° 09' N., Long. 108° 05' W., elev. 250 m. Active sand dunes.
yld5	Central Yakow Lake dune field. Lat. 59° 10' N., Long. 108° 00' W., elev. 240. Active sand dunes.
	D. cespitosa - dunes
asd1	Thomson Bay shoreline. Lat. 59° 05' N., Long. 109° 10' W., elev. 215 m. Moist beach habitat.
asd2	Beaver Point shoreline. Lat. 59° 08' N., Long. 108° 50' W., elev. 215 m. Moist beach habitat.
asd3	Wolverine Point shoreline. Lat. 59° 07' N., Long. 108° 20' W., elev. 215 m. Moist beach habitat.
	D. cespitosa - north
nor1	Buckinghorse River, B.C. Lat. 57° 25' N., Long. 122° 50' W., elev. 1010 m. Gravel and silt
nor2	Liard River, B.C. Lat. 59° 25' N., Long. 126° 00' W., elev. 520 m. Sandy floodplain.
nor3	Toad River, B.C. Lat. 59° 10' N., Long. 125° 50' W., elev. 855 m. Gravel floodplain.
nor4	South Kihanni Chief River, B.C. Lat. 57° 15' N., Long. 122° 40' W., elev. 795 m. Gravel
	D. cespitosa - central
cen1	Cypress Hills, Alberta. Lat. 49° 32' N., Long. 110° 21' W., elev. 1175 m. Moist prairie.
cen2	Gold Butte, Montana. Lat. 48° 45' N., Long. 111° 35' W, elev. 1375 m. Moist prairie.
cen3	Wainright, Alberta. Lat. 52° 45' N., Long. 110° 50' W., elev. 645 m. Wet parkland meadow.
cen4	Gooseberry Lake, Alberta. Lat. 52° 06' N., Long. 110° 45' W., elev. 703 m. Sandy beach habitat.
cen5	Webb, Saskatchewan. Lat. 50° 18' N., Long. 108° 13' W., elev. 735 m. Moist prairie.
cen6	Nose Hill, Alberta. Lat. 51° 08' N., Long. 114° 10' W., elev. 1285 m. Moist prairie.
cen7	Waiperous Creek, Alberta. Lat. 51° 25' N., Long. 115° 05' W., elev. 1500 m. Gravel floodplain.
cen8	Ghost River, Alberta. Lat. 51° 12' N., Long. 114° 40' W., elev. 1160 m. Gravel floodplain.
cen9	Kinky Lake, Alberta. Lat. 53° 17' N., Long. 117° 45' W., elev. 1130 m. Gravel beach habitat.
	D. cespitosa - south
sou1	Leadore, Idaho. Lat. 44° 41' N, Long. 113° 23' W, elev. 1810 m. Moist prairie.
sou2	Green River, Wyoming. Lat. 43° 17' N, Long. 109° 53' W, elev. 2435 m. Wet subalpine meadow.
sou3	Buffalo Springs, Colorado. Lat. 39° 02' N, Long. 106° 00' W, elev. 2885 m. Wet subalpine meadow.
sou4	Hoosier Pass, Colorado. Lat. 39° 21' N, Long. 106° 02' W, elev. 3600 m. Moist alpine meadow.

Genetic analysis. To provide a measure of the level of genetic variation within populations, the following statistics were computed: A, the mean number of alleles per locus; A_P, the mean number of alleles per polymorphic locus; P, the proportion of polymorphic loci when the most common allele has a frequency less than or equal to 0.95; and H_E, the expected panmictic heterozygosity. Values for A, A_P, P, and H_E were calculated at the species level, and for each population, which were then averaged for each species or geographic region. Species level statistics were calculated for the four genetic diversity parameters by treating all of the populations as if they were one population. *T*-tests were used to test for significant differences among these population parameters when only two comparisons could be made, whereas ANOVA followed by Student-Newman-

Keuls multiple range tests was employed when more than one comparison was to be made for a given population parameter.

The partitioning of genetic diversity within and among populations was analyzed using measures proposed by Nei (1973). We also calculated Wright's gene flow estimate [Nm_W, where $Nm_W = (1-G_{ST})/4G_{ST}$]; and Slatkin's gene flow estimate [Nm_S, where $\log_{10}(1) = a \log_{10}(Nm_S)+b$; a and b depend on the number of individuals sampled in each subpopulation, and (1) is the mean frequency of alleles unique to a single population] (Barton and Slatkin, 1986). The absolute population differentiation (D_M) was calculated using the formula: $D_M = sD_{ST}/(s-1)$ where s is the number of subpopulations in the analysis and D_{ST} is the among population genetic diversity (Nei, 1973).

Genetic identities (Nei, 1972) were calculated as well. Population variation statistics and standard genetic identities were calculated using the BIOSYS program (Swofford and Selander, 1989). Genetic diversity statistics were calculated using the GENESTAT-PC program (Whitkus, 1988). Principal components analysis (PCA) using the SYSTAT program (Wilkinson, 1990) helped evaluate the phenetic interpopulational relationships based on allele frequency distributions from polymorphic loci only. The PCA is presented with OTUs (populations) plotted onto the derived variables (principal axes) and alleles plotted at the end of vectors of the individual alleles relative to the PCA axes (FIGURE 3.2).

RESULTS

TABLE 3.2. Allele frequency data for polymorphic loci from 14 populations of *Deschampsia mackenzieana* and 20 populations of *D. cespitosa* used in this study. * indicates alleles unique to the sand dunes, ** indicates alleles unique to *D. cespitosa*.

Locus/	*D. mackenzieana*														*D. cespitosa* - dunes		
allele	wrd1	wrd2	tbd1	tbd2	tbd3	tbd4	cad1	cad2	cad3	yld1	yld2	yld3	yld4	yld5	asd1	asd2	asd3
Pgd-2																	
*a***	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.11	0.25
*b***	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
c	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.82	1.00	1.00	0.90	1.00	1.00	1.00	0.85	0.89	0.75
d	-	-	-	-	-	-	-	0.10	-	-	0.10	-	-	-	0.15	-	-
e	-	-	-	-	-	-	-	0.08	-	-	-	-	-	-	-	-	-
*f***	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Acp-2																	
*a***	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
b	0.02	-	-	-	-	-	-	-	0.05	-	-	-	-	0.02	-	0.06	-
c	0.94	0.95	0.85	0.77	0.97	0.95	0.98	1.00	0.87	0.98	0.95	1.00	0.95	0.90	0.92	0.75	0.56
d	0.05	0.05	0.15	0.24	0.03	0.05	0.02	-	0.08	0.02	0.05	-	0.05	0.09	0.04	0.14	0.34
*e***	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04	0.05	0.09
Acp-3																	
a	-	-	-	-	-	-	-	-	-	-	-	0.08	-	-	0.06	-	-

b	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.88	1.00	1.00	0.90	1.00	1.00
c**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
d	-	-	-	-	-	-	-	-	-	-	-	0.03	-	-	0.06	-	-
G3pdh-1																	
a**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
b	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Got-1																	
a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
b**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
c**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Idh-1																	
a**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
b	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.95	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.92	0.91
c*	-	-	-	-	-	-	-	0.05	-	-	-	-	-	-	-	0.08	0.09
Idh-2																	
a	-	0.35	-	0.56	-	0.48	-	0.47	-	-	0.30	-	0.66	0.52	-	-	-
b	1.00	0.65	1.00	0.44	1.00	0.52	1.00	0.53	1.00	1.00	0.70	1.00	0.34	0.48	1.00	1.00	1.00
c**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lap-2																	
a**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
b**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
c	0.06	0.20	0.45	0.06	0.47	-	0.06	0.50	-	-	0.83	0.80	0.33	0.05	0.31	0.13	0.19
d**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.11	0.30
e**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
f	0.94	0.80	0.55	0.94	0.53	1.00	0.94	0.50	1.00	1.00	0.17	0.20	0.67	0.95	0.69	0.77	0.52
g**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Me-2																	
a**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
b	1.00	0.92	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.92	1.00	0.86	0.65	0.73	0.69
c	-	0.08	-	-	-	-	-	-	-	-	-	0.08	-	0.14	0.35	0.27	0.31
Mnr-1																	
a**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
b**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03	-	0.02
c	0.89	0.30	0.27	0.38	0.33	0.33	0.25	0.40	0.85	0.69	0.35	0.40	0.27	0.69	0.83	0.83	0.80
d**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
e**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
f	0.11	0.70	0.73	0.62	0.67	0.67	0.75	0.60	0.15	0.31	0.65	0.60	0.73	0.31	0.15	0.17	0.19
g**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pgm-1																	
a**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
b	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
c**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pgm-2																	
a**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
b	0.56	1.00	0.95	1.00	1.00	1.00	1.00	0.92	1.00	0.63	0.88	0.70	1.00	1.00	0.32	0.86	0.86
c	0.44	-	0.05	-	-	-	-	0.08	-	0.38	0.12	0.30	-	-	0.68	0.14	0.14
d**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

TABLE 3.2. continued.

Locus/	*D. cespitosa* - north				*D. cespitosa* - central									*D. cespitosa* - south			
allele	nor1	nor2	nor3	nor4	cen1	cen2	cen3	cen4	cen5	cen6	cen7	cen8	cen9	sou1	sou2	sou3	sou4
Pgd-2																	
a**	-	0.37	0.33	-	-	-	-	-	-	-	-	-	-	0.03	-	-	-
b**	-	-	-	-	-	0.10	-	-	-	-	-	-	-	-	-	-	-
c	1.00	0.63	0.67	1.00	1.00	0.88	1.00	1.00	1.00	1.00	1.00	0.88	1.00	0.89	0.83	1.00	0.97
d	-	-	-	-	-	0.03	-	-	-	-	-	0.13	-	0.08	-	-	-
e	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03
f**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.17	-	-
Acp-2																	
a**	-	0.10	0.05	0.35	-	0.28	-	-	-	-	-	0.10	0.13	-	-	-	-
b	-	0.13	0.25	0.45	-	0.18	-	-	-	-	0.60	0.35	0.34	0.29	0.21	0.11	0.11
c	0.35	0.72	0.60	0.20	0.22	0.18	0.52	0.37	0.50	0.45	0.17	-	0.40	0.47	0.79	0.32	0.26
d	0.65	0.05	0.10	-	0.78	0.13	0.48	0.63	0.50	0.55	0.05	0.55	0.13	0.24	-	0.53	0.39
e**	-	-	-	-	-	-	-	-	-	-	0.17	-	-	-	-	0.03	0.26
Acp-3																	
a	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03	-	-
b	0.50	0.60	0.82	0.90	0.82	0.73	0.80	0.72	0.68	0.47	0.65	0.70	0.60	0.92	0.76	0.69	0.97
c**	0.28	0.40	0.17	-	-	0.08	0.09	0.15	0.18	0.39	0.13	-	0.19	0.08	0.05	0.31	0.03

d	0.22	-	-	0.10	0.17	0.20	0.09	0.15	0.13	0.13	0.22	0.30	0.21	-	0.18	-	-
G3pdh-1																	
a**	-	0.35	0.35	-	-	-	-	-	-	-	-	-	-	-	-	-	-
b	1.00	0.65	0.65	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Got-1																	
a	1.00	1.00	1.00	1.00	1.00	0.98	1.00	1.00	1.00	1.00	0.93	1.00	1.00	0.90	1.00	1.00	1.00
b**	-	-	-	-	-	-	-	-	-	-	0.08	-	-	0.10	-	-	-
c**	-	-	-	-	-	0.03	-	-	-	-	-	-	-	-	-	-	-
Idh-1																	
a**	-	-	-	-	-	-	0.02	0.03	-	0.05	-	-	-	-	-	-	-
b	1.00	1.00	1.00	1.00	1.00	1.00	0.98	0.98	1.00	0.95	1.00	1.00	1.00	1.00	1.00	1.00	1.00
c*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Idh-2																	
a	-	-	-	-	-	-	0.02	-	-	0.05	-	-	-	-	-	-	-
b	1.00	1.00	1.00	0.93	1.00	1.00	0.98	1.00	1.00	0.95	1.00	1.00	1.00	1.00	1.00	1.00	1.00
c**	-	-	-	0.08	-	-	-	-	-	-	-	-	-	-	-	-	-
Lap-2																	
a**	-	-	0.10	-	-	-	-	-	-	-	-	-	-	-	0.14	-	0.08
b**	-	-	-	0.48	-	-	-	-	-	-	-	-	0.21	0.45	0.35	-	-
c	-	-	-	-	-	0.05	-	-	0.18	-	0.20	-	-	-	-	0.18	-
d**	-	-	0.05	0.05	0.08	0.17	-	-	-	-	0.05	0.13	0.18	-	0.03	0.13	0.34
e**	1.00	0.73	0.82	0.42	0.93	0.70	1.00	1.00	0.82	1.00	0.73	0.88	0.61	0.55	0.46	0.55	0.55
f	-	0.27	0.03	0.05	-	-	-	-	-	-	0.03	-	-	-	-	-	-
g**	-	-	-	-	-	0.08	-	-	-	-	-	-	-	-	-	0.13	0.03
Me-2																	
a**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03	-	-
b	0.75	0.65	0.85	0.92	1.00	1.00	0.87	1.00	0.87	0.89	0.93	1.00	0.61	0.63	0.79	1.00	1.00
c	0.25	0.35	0.15	0.08	-	-	0.13	-	0.13	0.11	0.08	-	0.39	0.37	0.18	-	-
Mnr-1																	
a**	-	-	-	-	0.03	-	-	-	-	0.22	0.07	-	0.03	-	-	-	-
b**	0.05	-	-	0.05	0.03	0.17	-	0.08	0.03	0.08	0.02	0.03	0.05	-	-	0.13	0.05
c	0.82	0.55	0.50	0.67	0.75	0.72	0.83	0.77	0.87	0.53	0.67	0.82	0.79	0.39	0.76	0.74	0.71
d**	-	-	0.03	-	-	-	-	-	-	-	-	-	0.03	-	-	-	0.08
e**	0.13	0.03	-	0.12	0.15	0.08	0.07	0.03	-	0.16	0.03	0.17	-	-	-	0.13	0.16
f	-	-	-	-	-	-	0.06	0.03	0.11	-	-	-	-	-	-	-	-
g**	-	0.42	0.47	0.15	-	0.03	0.02	-	-	-	-	-	-	0.61	0.26	-	-
Pgm-1																	
a**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.13
b	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.76
c**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.11
Pgm-2																	
a**	-	0.42	0.35	-	-	-	-	-	-	-	-	-	-	-	-	-	-
b	0.95	0.58	0.65	0.90	1.00	0.87	0.89	0.75	0.92	1.00	0.93	1.00	0.89	0.89	0.85	1.00	0.92
c	0.05	-	-	0.10	-	0.13	0.07	0.25	0.08	-	0.08	-	0.08	0.11	0.08	-	0.08
d**	-	-	-	-	-	-	0.02	-	-	-	-	-	0.03	-	0.08	-	-

The 13 enzyme systems assayed in this study are coded by 20 putative loci. Some isozymes were excluded from our analysis because they had complex banding patterns or overlapped with other loci (PGI, MDH, SKD). Eight of the loci were monomorphic in all populations: *Pgd-1*, *Acp-1*, *Acp-4*, *G3pdh-2*, *Got-2*, *Lap-1*, *Me-1*, *Pgi-1*. Twelve loci, *Pgd-2*, *Acp-2*, *Acp-3*, *G3pdh-1*, *Got-1*, *Idh-1*, *Idh-2*, *Lap-2*, *Me-2*, *Mnr-1*, *Pgm-1*, and *Pgm-2*, were polymorphic in at least some populations (Table 3.2).

There were 50 alleles at the 12 polymorphic loci (Table 3.2). No alleles were restricted to the endemic taxon but *Idh-1c* was restricted to the sand dune populations of both species, occurring in at least some populations of *Deschampsia mackenzieana* and *D. cespitosa* with a frequency greater than 0.05. Three alleles not found in the endemic species, *Pgd-2a*, *Acp-2e*, and *Lap-2d*, were found in *D. cespitosa* populations from both sand dune and non-sand dune habitats. Eighteen other alleles were found only in *D. cespitosa* populations in non-sand dune habitats. At ten polymorphic loci the endemic species shared the same most common allele with populations of the progenitor species. *Lap-2f* was the most common allele in *D. mackenzieana* and *D. cespitosa* populations from the sand dunes, whereas *Lap-2e* was the most common allele in the progenitor populations from non-sand dune habitats. Mean allele frequencies indicated populations of *D. mackenzieana* and *D. cespitosa* differed for the most common allele at only one locus (*Mnr-1f* vs. *Mnr-1c*).

Deschampsia mackenzieana had considerably less genetic variation than *D. cespitosa*. At the population level, the endemic species had lower average A (1.22 vs. 1.52), A_P (2.17 vs. 2.70), P (18.9 vs. 30.5), and H_E (0.062 vs. 0.119) than the widespread progenitor species (TABLE 3.3, $P < 0.01$). Values for A, A_P, and P were significantly less at the species level in *D. mackenzieana* than in *D. cespitosa* (TABLE 3.3). Subdividing the progenitor populations into geographic regions revealed similar amounts of genetic variation for populations in all four regions. In all comparisons, *D. mackenzieana* had less genetic diversity than *D. cespitosa* populations from any given geographic region (TABLE 3.3).

TABLE 3.3. Summary of allozyme variation for 20 loci within 14 populations of the endemic *Deschampsia mackenzieana* and 20 populations of the widespread *D. cespitosa* from four geographic regions. A locus was considered polymorphic if the most common allele frequency was less than 0.95.[1,2]

Population	N	A	A_P	P	H_E
		D. mackenzieana			
wrd1	32	1.25	2.25	20	0.047
wrd2	30	1.20	2.00	20	0.072
tbd1	30	1.20	2.00	20	0.062
tbd2	17	1.20	2.00	20	0.074
tbd3	32	1.15	2.00	10	0.051
tbd4	30	1.15	2.00	15	0.054
cad1	32	1.15	2.00	10	0.027
cad2	30	1.35	2.17	30	0.104
cad3	29	1.30	2.20	25	0.073
yld1	30	1.15	2.50	10	0.026
yld2	32	1.15	2.50	10	0.047
yld3	30	1.30	2.50	30	0.083
yld4	30	1.25	2.00	25	0.081
yld5	32	1.25	2.25	20	0.070
Mean		1.22a	2.17a	18.9a	0.062a
(SE)		0.02	0.05	1.9	0.006
		D. cespitosa - dunes			
asd1	36	1.50	2.43	35	0.112
asd2	32	1.50	2.43	35	0.104

asd3	32	1.50	2.43	35	0.139
Mean		1.50b	2.43ab	35.0b	0.118b
(SE)		0.00	0.00	0.0	0.011
		D. cespitosa - north			
nor1	30	1.35	2.40	25	0.095
nor2	30	1.55	2.37	40	0.189
nor3	30	1.65	2.63	40	0.168
nor4	30	1.60	2.71	35	0.122
Mean		1.54b	2.53ab	35.0b	0.144b
(SE)		0.07	0.08	3.5	0.021
		D. cespitosa - central			
cen1	30	1.30	2.50	20	0.062
cen2	30	1.75	3.33	30	0.139
cen3	27	1.50	2.80	25	0.084
cen4	30	1.40	2.75	20	0.091
cen5	31	1.40	2.33	30	0.095
cen6	32	1.45	2.50	30	0.109
cen7	30	1.70	3.00	35	0.124
cen8	30	1.38	2.40	25	0.090
cen9	31	1.65	3.17	30	0.143
Mean		1.50b	2.75b	27.2b	0.104b
(SE)		0.05	0.12	1.7	0.009
		D. cespitosa - south			
sou1	31	1.50	2.25	40	0.142
sou2	33	1.65	2.85	35	0.138
sou3	31	1.45	3.25	20	0.105
sou4	31	1.70	3.40	25	0.121
Mean		1.58b	2.94b	30.0b	0.127b
(SE)		0.06	0.26	4.6	0.009
		D. mackenzieana			
population	29.7	**1.22	**2.17	**18.9	**0.062
(SE)	-	0.02	0.05	1.9	0.006
species	416	*1.55	**2.22	45	0.083
(SE)	-	0.15	0.15	-	0.034
		D. cespitosa - all			
population	30.8	**1.52	**2.70	**30.5	**0.119
(SE)	-	0.03	0.09	1.6	0.007
species	617	*2.90	**4.17	60	0.148
(SE)	-	0.46	0.49	-	0.049

[1] Mean number of alleles per locus (A), mean number of alleles per polymorphic locus (A_P), percent polymorphic loci (P), mean expected heterozygosity (H_E).

[2] Lowercase letters indicate values differ between groups for population genetic statistics ($P < 0.05$).

* and ** indicate values differ between species at $P < 0.05$ and $P < 0.01$, respectively. Species level genetic diversity values were calculated by treating all populations within the species as one population.

Total genetic diversity at polymorphic loci (H_T) for *Deschampsia mackenzieana* was 0.189, but the proportion of allozyme diversity among populations (G_{ST}) was 0.268, indicating that there was considerable genetic differentiation among populations (TABLE 3.4). *Deschampsia cespitosa* had a higher mean total genetic diversity ($H_T = 0.249$) than *D. mackenzieana*, but a lower amount of population differentiation ($G_{ST} = 0.212$), despite the much larger geographic collecting range. An analysis of the progenitor populations subdivided on the basis of geographic region indicates that *D. cespitosa* maintains higher total- and within-population genetic diversity than the endemic *D. mackenzieana*. Values for G_{ST} are lower for all geographic subdivisions of the progenitor when compared to the endemic taxon (TABLE 3.4).

TABLE 3.4. Nei's (1973) statistics of genetic diversity and estimates of gene flow for Deschampsia mackenzieana and four groups of D. cespitosa. Values presented are means over all polymorphic loci within a species or geographic group.[1]

	Number of							
Species and region	Pops.	Loci	H_T	H_S	G_{ST}	Nm_W	Nm_S	D_M
D. mackenzieana	14	9	0.189	0.138	0.268	0.684	1.636	0.054
D. cespitosa	20	12	0.249	0.196	0.212	0.933	0.850	0.055
- dunes	3	6	0.333	0.294	0.116	1.915	0.959	0.058
- north	4	9	0.399	0.318	0.202	0.991	0.212	0.107
- central	9	10	0.232	0.205	0.116	1.898	0.779	0.030
- south	4	9	0.332	0.280	0.157	1.349	0.658	0.070

[1] H_T = total gene diversity; H_S = gene diversity within populations; G_{ST} = the proportion of total gene diversity found among populations; Nm_W = Wright's gene flow estimate; Nm_S = Slatkin's gene flow estimate; and D_M = absolute population differentiation.

Nm_W estimates were lower for *Deschampsia mackenzieana* than for *D. cespitosa* (TABLE 3.4), whereas Nm_S estimates were higher for the tetraploid endemic than the diploid progenitor. The absolute measure of genetic differentiation among populations (D_M) was similar between *D. mackenzieana* and *D. cespitosa* (TABLE 3.4).

TABLE 3.5. Matrix of gene identities (Nei, 1972) averaged over populations of *Deschampsia mackenzieana* and *D. cespitosa* from four geographic regions. Ranges are given in brackets.

Species	1	2	3	4	5
D. mackenzieana	0.976 (0.943-1.000)				
D. cespitosa - dunes	0.962 (0.926-0.993)	0.983 (0.972-0.996)			
D. cespitosa - north	0.912 (0.878-0.943)	0.935 (0.905-0.954)	0.958 (0.940-0.994)		
D. cespitosa - central	0.915 (0.878-0.943)	0.935 (0.893-0.962)	0.966 (0.932-0.995)	0.985 (0.969-0.999)	
D. cespitosa - south	0.929 (0.903-0.955)	0.949 (0.921-0.966)	0.966 (0.936-0.988)	0.975 (0.955-0.994)	0.973 (0.962-0.990)

Genetic identities among the *Deschampsia mackenzieana* populations ranged from 0.943 to 1.000 with a mean of 0.976 (TABLE 3.5). Genetic identities among the *D. cespitosa* populations ranged from 0.893 to 0.999 (TABLE 3.5). *Deschampsia mackenzieana* had highest genetic identities with the progenitor populations of *D. cespitosa* from the Athabasca sand dunes and lowest genetic identities with progenitor populations from the northern and central geographic regions (TABLE 3.5). *Deschampsia cespitosa* populations from the sand dunes had higher interspecific genetic identities with the sympatric endemic taxon (0.962) than intraspecific identities with allopatric populations of *D. cespitosa* (0.935 to 0.949) (TABLE 3.5). The PCA of allele frequencies also indicated the close genetic relationship of the sympatric *D. mackenzieana* to *D. cespitosa* populations from the Athabasca sand dunes (FIGURE 3.2). There was no strong association of *D. cespitosa* populations from the north, central, and south geographic regions with populations from their respective geographic region (FIGURE 3.2). The PCA revealed that *Lap-2*, *Acp-2*, and *Acp-3* were the loci that differentiated the sand dune populations of both *D. mackenzieana* and *D. cespitosa* from other progenitor populations (FIGURE 3.2).

DISCUSSION

Amount and pattern of genetic diversity. *Deschampsia mackenzieana* is both a recently evolved species and a narrow endemic. Evidence from population genetic studies suggests derivative species have lower amounts of genetic diversity than their progenitors (Gottlieb, 1973, 1974; Crawford and Smith, 1982a, 1982b; Crawford, Ornduff, and Vasey, 1985; Pleasants and Wendel, 1989; Purdy, Bayer, and Macdonald, 1994 [chapter 2]). In addition, plant species with limited geographic ranges typically have lower levels of genetic polymorphism (Karron, 1987; Loveless and Hamrick, 1988; Hamrick and Godt, 1989; Pleasants and Wendel, 1989; Falk and Holsinger, 1991; Sherman-Broyles et al., 1992), although not always (Bayer and Crawford, 1986; Karron et al. 1988; Linhart and Premoli, 1993).

Deschampsia mackenzieana has considerably less genetic diversity at the species and population levels than the widespread progenitor *D. cespitosa*, which supports the trend seen in the majority of studies. Levels of genetic variation (A, P, H_E) in *D. cespitosa* were comparable to other species with similar life history characteristics: monocots, widespread geographic range, boreal-temperate distribution, wind-pollinated (Hamrick and Godt, 1989). Although *D. cespitosa* occurs over a wide range of habitats and geographic regions, genetic diversity was comparable among sand dune, northern, central, and southern regions for A, A_P, P, and H_E. *Deschampsia mackenzieana* had significantly lower levels of population and species level genetic diversity than its widespread progenitor, but comparable with the mean values for other endemic taxa (Hamrick and Godt, 1989).

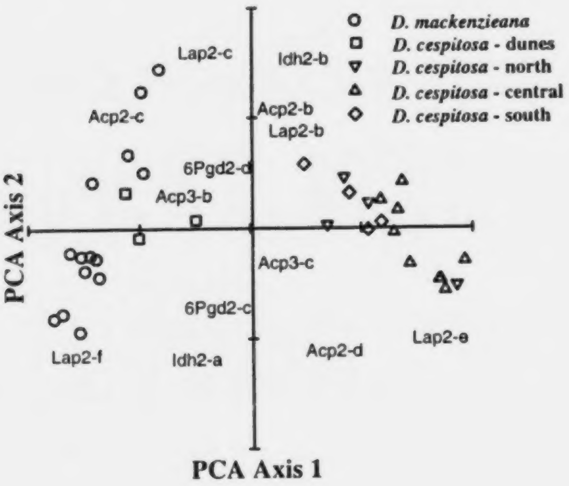

FIGURE 3.2. Principal components analysis of allele frequencies from populations of the endemic *Deschampsia mackenzieana* and the widespread *D. cespitosa*. The first two principal components explain 60.8 and 9.6 % of the variance, respectively. Positions for OTUs (populations) and variables (alleles) are presented.

The observed reduction in genetic polymorphism in the endemic taxon may be due to founder effect, genetic drift, strong directional selection, and/or a change in breeding system (Karron, 1987). *Deschampsia cespitosa* is known to be self-incompatible (Rothera and Davy, 1986; Bush and Barrett, 1993), and our attempts to produce offspring as a result of selfing in *D. mackenzieana* were unsuccessful. Consequently, *D. mackenzieana* and *D. cespitosa* probably have similar rates of outcrossing. Because the endemic taxon maintains large and extensively distributed populations within its restricted range (Raup and Argus, 1982), genetic drift is unlikely to account for the loss of genetic diversity observed. In light of these facts (Barrett and Kohn, 1991), a genetic bottleneck in the founding population of *D. mackenzieana* is the most likely explanation for the reduced levels of species and population level genetic variation. However, because of differences in habitats of the two species, strong directional selection cannot be ruled out as a factor resulting in the reduction of genetic diversity in *D. mackenzieana*.

Deschampsia cespitosa had considerably higher total- (H_T) and within-population (H_S) genetic diversity than the endemic *D. mackenzieana*, a trend seen in other studies (Hamrick and Godt, 1989). Interestingly, populations of *D. mackenzieana*, despite being collected over a very small geographic area, exhibited higher populational differentiation (G_{ST}) than any regional group of *D. cespitosa*. The three populations of the progenitor taxon collected from the sand dunes over a distribution similar to the endemic had very low levels of population differentiation. This result differs from that seen in most studies where endemic taxa generally partition their genetic diversity in the same pattern as related widespread taxa (Hamrick and Godt, 1989). Values of G_{ST} are relative and depend on the amount of genetic diversity present (Nei, 1973). The absolute measure of population differentiation (D_M) revealed that differences between populations of *Deschampsia mackenzieana* are of the same magnitude as differences between populations of the genetically diverse *D. cespitosa*.

Estimates of gene flow among populations of *Deschampsia mackenzieana* differ significantly depending on the method used to calculate the parameter. Wright's estimate of gene flow (Nm_W), which is derived from the value of G_{ST}, is lower for the endemic than any group of *D. cespitosa*. In contrast, Slatkin's estimate of gene flow (Nm_S), based on the number of private alleles in populations, suggests higher gene flow for *D. mackenzieana* than any group of *D. cespitosa*. This suggests the private alleles that occur in the endemic have very low frequencies, and that most of the differentiation seen in *D. mackenzieana* is attributed to frequency differences of alleles that are found in more than one population.

Origin of Deschampsia mackenzieana. There are a number of predictions that have been made regarding the relationship between progenitor and derivative taxa (Gottlieb, 1973; Pleasants and Wendel, 1989), all of them met in this study. First, the intraspecific identities among populations of *Deschampsia mackenzieana* were similar to the interspecific identities with populations of *D. cespitosa* from the sand dunes. Second, the sand dune populations of *D. cespitosa* had higher identities with the endemic taxon than with other populations of the same species. Third, there was less genetic variation in the derivative taxon than that found in the progenitor. Fourth, the allelic diversity in *D. mackenzieana* is a subset of the gene pool of *D. cespitosa*, and there are no alleles unique to the derivative species, likely due to inadequate time for mutations to accumulate.

The data suggest that *Deschampsia mackenzieana* may be derived from the gene pool of sympatric *D. cespitosa* populations that occurred on the Athabasca sand dunes during speciation and that *D. mackenzieana* is a recently derived species (Crawford, 1983). *Deschampsia mackenzieana* probably functions as a distinct species with its own gene pool due to the reproductive barrier resulting from different ploidy levels. Morphological and cytological hybrids have not been found on the sand dunes despite the co-occurrence of *D. cespitosa* and *D. mackenzieana* in a number of locations (B. Purdy, personal observation).

Effects of polyploidy. Two chromosomal races ($2n = 26, 52$) of *Deschampsia cespitosa* have been reported from Britain (Rothera and Davy, 1986). Cytological evidence (Rothera and Davy, 1986) and isozyme data (Bush and Barrett, 1993) suggest that the diploid cytotypes ($2n = 26$) are, in fact, ancient tetraploids. Reports on the inheritance of isozymes in *D. cespitosa* have differed (Gehring and Linhart, 1992; Bush and Barrett, 1993). Colorado populations of *D. cespitosa* were found to have a disomic pattern of inheritance at all isozyme loci investigated (Gehring and Linhart, 1992). Ontario populations of *D. cespitosa* had this pattern of inheritance at some loci, whereas other loci revealed complex banding patterns indicating gene duplication, with isozymes of PGD, PGI, MDH, and DIA appearing to be duplicated (Bush and Barrett, 1993).

In our study, PGI and MDH produced complex banding patterns and appeared to be duplicated based on the occurrence of interlocus heteromeric molecules. These isozymes were excluded from further genetic analysis. However, in the western North American populations of *Deschampsia cespitosa* used in our study, PGD did not appear to be duplicated. Segregation patterns of open pollinated progeny arrays revealed a disomic pattern of inheritance of isozymes in the diploid *D. cespitosa*, similar to that reported by Gehring and Linhart (1992), and a tetrasomic pattern of inheritance in the tetraploid *D. mackenzieana*.

Polyploidy is now regarded to be an integral component of the ecological and evolutionary dynamics of plant populations and species (Thompson and Lumaret, 1992). Central questions regarding polyploidy include the processes responsible for the origin of polyploids, ecological conditions favoring the establishment and coexistence of different cytotypes, and colonization patterns of newly formed polyploids.

Electrophoretic investigations have focused on determining the parentage of polyploids, whether the polyploids were allotetraploids or autotetraploids in origin, and amounts of divergence among cytotypes or potential amounts of gene flow across cytotypes (Roose and Gottlieb, 1976; Bayer and Crawford, 1986; Bryan and Soltis, 1987; Rieseberg and Warner, 1987; Gastony, 1990; Ashton and Abbott, 1992). Polyploidy is a mechanism that allows plants to increase heterozygosity and hence, genetic diversity. This is especially true in small populations where the effects of genetic drift could be compensated for by the added heterozygosity that both autopolyploids and allopolyploids possess. The majority of isozyme studies on diploid and polyploid derivatives have found polyploids to have higher heterozygosity, higher number of alleles per locus, and more polymorphic loci than their diploid progenitors (Soltis and Rieseberg, 1986; Bayer, 1989; Soltis and Soltis, 1989; Cai, Macdonald, and Chinnappa, 1990; Lumaret and Barrientos, 1990; Watson, Elisens, and Estes, 1991).

Deschampsia mackenzieana does not follow this trend and is genetically depauperate when compared to its diploid progenitor. Although formal genetic analysis of progeny from controlled crosses was not performed in this study, the following points suggest that *D. mackenzieana* is an autotetraploid. Fixed heterozygosity was not seen at any locus, the same number of loci were observed in the diploid and tetraploid cytotypes, and, in progeny arrays from naturally outcrossed mother plants, segregation of heterozygotes into balanced and unbalanced heterozygotes as well as homozygotes (i.e., tetrasomic inheritance) was observed. Although autotetraploids are thought to be less common than allotetraploids, they have been observed to maintain higher genetic diversity than their diploid progenitors (Soltis and Rieseberg, 1986; Soltis and Soltis, 1989; Lumaret and Barrientos, 1990).

Gene flow with diploid progenitor populations was probably important for the high levels of genetic diversity noted in the tetraploid *Dactylis glomerata* (Lumaret and Barrientos, 1990). A genetic bottleneck in the founding population of *Deschampsia mackenzieana*, coupled with minimal gene flow with the genetically diverse diploid cytotypes of *D. cespitosa*, might be responsible for the small gene pool observed in this sand dune endemic. In addition, the low levels of genetic diversity in *D. mackenzieana* may suggest a single polyploidization event leading to the species origin.

Niche differentiation is thought to be required for the coexistence of newly formed polyploids with their diploid progenitors (Thompson and Lumaret, 1992) and has been demonstrated in the *Antennaria rosea* complex (Bayer, Purdy, and Lebedyk, 1991), *Dactylis glomerata* (Lumaret et al., 1987), and *Deschampsia cespitosa* (Rothera and Davy, 1986). In each of these studies, the tetraploid cytotypes were more common in disturbed habitats. In Britain, *D. cespitosa* diploid plants were more common in woodlands whereas tetraploid plants dominate in areas where disturbance has recently or historically occurred (Rothera and Davy, 1986). On the Athabasca sand dunes, the tetraploid *D. mackenzieana* clearly occupies the disturbed habitat of active sand dunes whereas the diploid *D. cespitosa* occurs primarily on stabilized moist sand habitats along the shores of lakes and rivers. Tetraploid *Dactylis glomerata* (Lumaret and Barrientos, 1990) flowered earlier than diploid cytotypes, an observation that is consistent with phenological observations made on populations of *Deschampsia mackenzieana* and *D. cespitosa* from the Athabasca sand dunes (B. Purdy, personal observation).

Unlike the studies on *Dactylis glomerata* in Spain (Lumaret and Barrientos, 1990) and *Deschampsia cespitosa* in Britain (Rothera and Davy, 1986), the diploid *D. cespitosa* and the tetraploid *D. mackenzieana* are morphologically distinct (Raup, 1936; Kawano, 1963). *Deschampsia mackenzieana* differs from *D. cespitosa* in having larger, only two flowered spikelets, and in its spreading panicles (Raup, 1936). The endemic species also differs from *D. cespitosa* in having smooth lemmas with awns attached near the middle, instead of scabrous lemmas with awns from near the base, and in having strongly involute leaves with short ligules instead of flat leaves with longer ligules (Raup, 1936). The morphological distinctness of *D. mackenzieana* is maintained when grown in the same habitat as *D. cespitosa* (B. Purdy, personal observation), despite the high amounts of phenotypic plasticity observed in the diploid *D. cespitosa* (Rothera and Davy, 1986). Yet, the close genetic relationship between diploid populations of *D. cespitosa*, in particular those populations from the Athabasca sand dunes, and the tetraploid *D. mackenzieana*, suggests a close phylogenetic relationship.

Conclusions. *Stellaria arenicola* was previously the only Athabasca sand dune endemic that has been the subject of a population genetic investigation (Purdy, Bayer, and Macdonald, 1994 [chapter 2]). Although *S. arenicola* was found to have less genetic diversity than its closely related geographically widespread progenitor taxon, *S. longipes*, the sympatric progenitor populations were thought to play a role in providing genetic variation to the endemic populations. The genetic isolation experienced in *Deschampsia mackenzieana* due to its tetraploid cytology is likely responsible for the marked reduction in genetic diversity found within populations of the endemic species. *Deschampsia mackenzieana* is well adapted to the active sand dune habitat, and is one of the most important dune stabilizing species on the Athabasca sand dunes (Raup and Argus, 1982). However, as a result of speciation on the Athabasca sand dunes, *D. mackenzieana* may have a reduced ability for future evolution, unless opportunities arise for the immigration of new allelic diversity into future populations.

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Chapter Four

Allozyme variation in the Athabasca sand dune endemic, *Salix silicicola*, and the closely related widespread species, *S. alaxensis* (Salicaceae) [1]

ABSTRACT. Genetic variation was estimated by starch gel electrophoretic resolution of 17 putative isozyme loci in eight populations of the Athabasca sand dune endemic *Salix silicicola* from northern Saskatchewan, Canada, and five populations of its putative progenitor species, *Salix alaxensis*, from northern British Columbia, Canada. Thirty-seven alleles were detected at ten polymorphic loci. Six loci were polymorphic in the endemic species and ten loci were polymorphic in the presumed progenitor species. *Salix silicicola* had one unique allele, whereas *Salix alaxensis* had 17 alleles not found in the former species. Populations of the endemic contained fewer alleles per locus (1.30 vs. 1.85), fewer alleles per polymorphic locus (2.05 vs. 2.85), lower percent polymorphic loci (28.7 vs. 45.9) and lower genetic diversity (0.073 vs. 0.195) than did populations of the putative progenitor species. Genetic identities within species averaged 0.981 for *Salix silicicola* and 0.973 for *Salix alaxensis* and between species identities ranged from 0.902 to 0.963 with a mean of 0.932. At polymorphic loci, total gene diversity was relatively high in *Salix silicicola* ($H_T = 0.305$) and *Salix alaxensis* ($H_T = 0.384$). Population differentiation was relatively low in both species (*Salix silicicola*, $G_{ST} = 0.159$; *Salix alaxensis*, $G_{ST} = 0.097$) whereas estimates of gene flow based on G_{ST} values were moderate (*Salix silicicola*, $Nm_W = 1.32$; *Salix alaxensis*, $Nm_W = 2.33$), consistent with these trees' dioecious breeding system and wind-dispersed seeds.

INTRODUCTION

The amount and pattern of genetic variation within and among populations and closely related species can be influenced by a wide range of factors, including mating system, natural selection, geographic distribution, and historical events (Loveless and Hamrick, 1988). Plant species with limited geographic ranges typically have lower levels of genetic diversity than do widespread taxa (Karron, 1987; Hamrick and Godt, 1989). In general, endemic species contain fewer polymorphic loci, fewer alleles per polymorphic locus, and less heterozygosity than do more widespread species (Hamrick and Godt, 1989). This paucity of genetic diversity may be due to stochastic processes, such as genetic drift and founder effects, and/or strong directional selection toward genetic uniformity (Karron, 1987). Recently-evolved species are often classified as narrow endemics because of their restricted geographic ranges.

Although the number of plant allozyme studies of genetic diversity in rare and endemic taxa has increased in recent years (Hamrick and Godt, 1989), there are few studies of endemic and widespread taxa that are closely related, especially species pairs which are progenitors-derivatives as well (Edwards and Wyatt, 1994). Population genetic studies have revealed that derivative species generally harbor less genetic diversity than the progenitor (Gottlieb, 1973, 1974; Crawford and Smith, 1982a, 1982b; Crawford, Ornduff, and Vasey, 1985; Loveless and Hamrick, 1988; Pleasants and Wendel, 1989), though not always (Gottlieb, Warwick, and Ford, 1985; Linhart and Premoli, 1993). Information on the genetic diversity of rare and endangered species is an important factor for determining approaches to conservation (Soulé and Kohm, 1989).

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[1] A version of this chapter has been published. Purdy and Bayer, 1995. *Systematic Botany* 20: 179-190.

The flora of boreal and arctic regions typically contain few endemic taxa because of the short time period available, since the Pleistocene, for speciation to occur (Kruckeberg and Rabinowitz, 1985). Yet, the Athabasca sand dunes in northern Saskatchewan, Canada, contain a number of rare plant species, including ten endemic taxa (Raup, 1936; Raup and Argus, 1982). Previous investigations on the population genetics of Athabasca sand dune endemics *Stellaria arenicola* Raup (Purdy, Bayer, and Macdonald, 1994 [chapter 2]) and *Deschampsia mackenzieana* Raup (Purdy and Bayer, 1995 [chapter 3]) focused on species that evolved while sympatric with their progenitor taxon. The tetraploid nature of *D. mackenzieana* isolated it from the diploid *D. cespitosa* (L.) Beauv., with genetic diversity in the tetraploid being considerably lower than in its progenitor (Purdy and Bayer, 1995 [chapter 3]). *Stellaria arenicola* had lower genetic diversity than did *S. longipes* Goldie, the species from which it evolved, but gene flow between species may have been important in maintaining higher levels of genetic variation in this endemic (Purdy, Bayer, and Macdonald, 1994 [chapter 2]).

Salix silicola

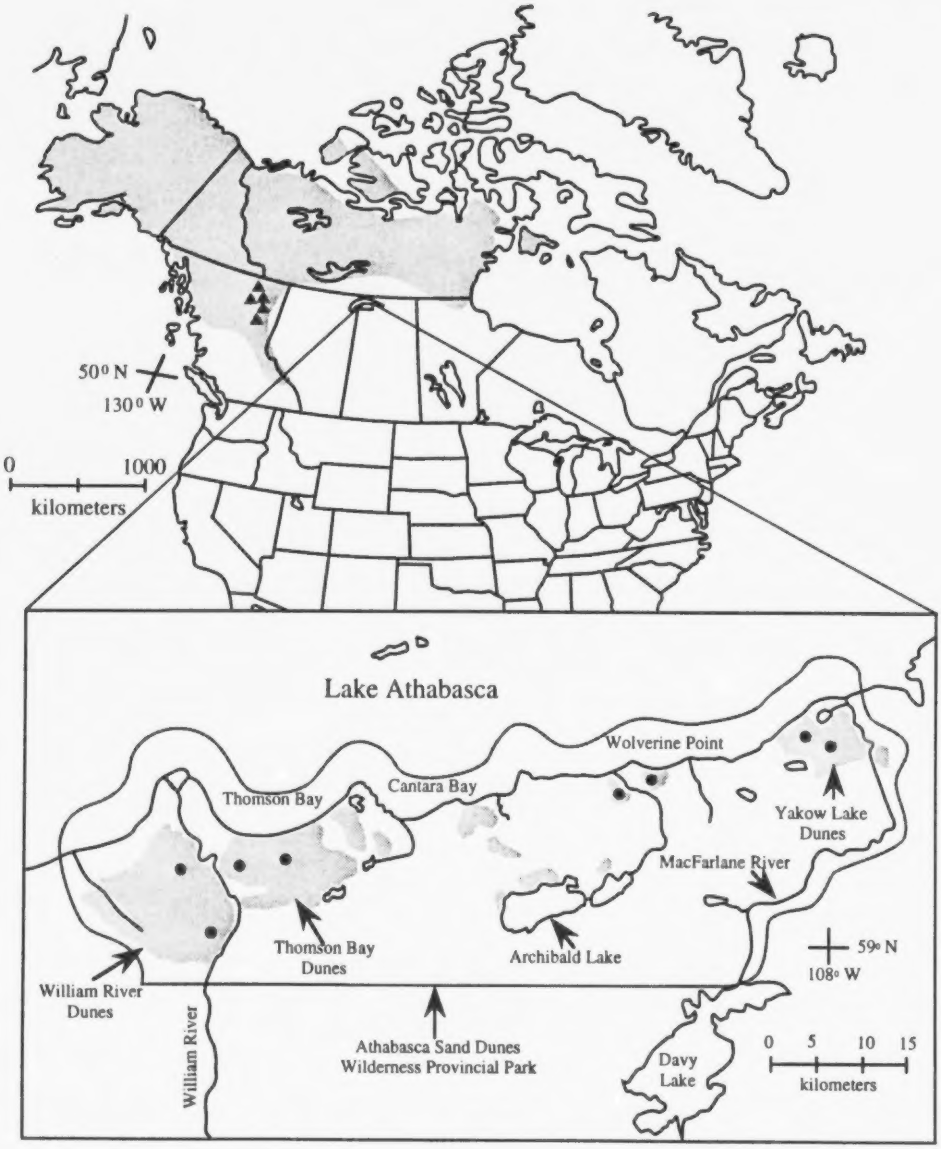

FIGURE 4.1. Location of populations of the widespread *Salix alaxensis* (triangles) and the Athabasca sand dune endemic *S. silicicola* (circles) sampled in this study. The shaded area represents the North American distribution for *S. alaxensis*.

Salix silicicola Raup, one of four endemic willows of the Athabasca sand dunes, is restricted to the active sand dunes, gravel pavements, and beach ridges on the south shore of Lake Athabasca (Raup, 1936, 1959). A conspicuous willow, it is thought to be derived from *S. alaxensis* (Anders.) Cov., from which it differs by its short stipules (up to 7 mm. long, compared to 22 mm.) that are broadly ovate to lanceolate rather than linear-lanceolate to filiform, and by its persistent, heavy, hairy-tomentose vestiture on both sides of the laminae instead of being glabrous or glabrate and bright green on the upper surface (Raup, 1959). *Salix alaxensis*, a common willow in Alaska, Yukon, Northwest Territories, and the northern Rocky Mountains in British Columbia (Raup, 1959), occurs with other pioneer vegetation on river alluvia, glacial moraines, immature forests, and alpine tundra (Argus, 1973). Populations of *S. silicicola* are allopatric with populations of *S. alaxensis* at present (Argus and Steele, 1979; Porsild and Cody, 1980).

This study was conducted to compare the amount and pattern of genetic diversity of *Salix silicicola*, a recently evolved narrow endemic, with *S. alaxensis*, its presumed widespread progenitor. This is the first study of an endemic from the Athabasca sand dunes that has an allopatric distribution with its presumed progenitor. We compared our results with studies of other endemic species from the Athabasca sand dunes that have evolved in sympatry with their progenitor taxon. We also wanted to confirm the close genetic relationship of the two taxa as well as to establish population genetic information for *S. silicicola*, a candidate for the endangered species list in Canada.

MATERIALS AND METHODS

Sample Collection. Summer cuttings from two or three year old stems were collected from five populations of *S. alaxensis* from northern British Columbia and eight populations of *Salix silicicola* on the Athabasca sand dunes in Saskatchewan (FIGURE 4.1; TABLE 4.1). The cuttings were wrapped in live *Sphagnum* and kept moist and cool until they were transported to the University of Alberta greenhouse. After being planted in soil in Spencer-Lemaire containers, the cuttings were placed on a mist bench until leaves began to emerge. At least 50 stems were collected from each population, although a reduced number of cuttings actually grew new leaves (TABLE 4.3).

Electrophoresis. Standard methods for starch gel electrophoresis were employed in this study (Soltis et al., 1983). Fresh pieces of actively growing leaf tissue were ground in cold Tris-HCl extraction buffer (Purdy, Bayer, and Macdonald, 1994 [chapter 2]). The supernatant was absorbed onto filter paper wicks, frozen at -20° C overnight, and electrophoresed the following morning. The filter paper wicks were loaded onto 12% electrolyzed potato starch gels (Sigma Chemical, St. Louis, MO).

Three buffer systems were used to resolve 11 enzyme systems in this study. Glutamate oxalate-transaminase (GOT) and glutamate dehydrogenase (GDH) were resolved on the buffer system VI of Soltis et al. (1983). Acid phosphatase (ACP), glucose-6-phosphate dehydrogenase (G6PDH), leucine aminopeptidase (LAP), and phosphoglucose isomerase (PGI) were resolved on the buffer system VII of Soltis et al. (1983). 6-phosphogluconate dehydrogenase (PGD), glyceraldehyde-3-phosphate dehydrogenase (G3PDH), isocitrate dehydrogenase (IDH), menadione reductase (MNR), and shikimic acid dehydrogenase (SKD) were resolved on a histidine - citric acid buffer system (Cardy, Stuber, and Goodman, 1983). The first two buffer systems were run at 50 mA for 30 min, then at 60mA for 4-5 hr, the third buffer system was run at 30 mA for 4-5 hr. The electrophoresis was performed at 4° C.

Enzymatic assays followed Soltis et al. (1983), except for MNR (Wendel and Weeden, 1989). For enzymes with more than one putative locus, the staining zones were numbered sequentially, with the most anodally migrating isozyme designated as 1, the next 2, and so on. Similarly, the most anodal allozyme of a gene was labeled A, etc. Bands were categorized as isozymes and allozymes by observing segregation of bands among individuals in the populations sampled in light of the typical subunit structure and subcellular compartmentalization (Gottlieb, 1981; Weeden and Wendel, 1989). Genotype frequencies at each locus were determined for each population.

TABLE 4.1. Population designation, collection location, and habitat for eight populations of *Salix silicicola* and five populations of *S. alaxensis* used in this study.

Population	Population location and habitat
	S. silicicola
WRD1	Central William River dune field. Lat. 59° 03' N., Long. 109° 15' W., elev. 244 m. Gravel
WRD2	South William River dune field. Lat. 58° 55' N., Long. 109° 12' W., elev. 275 m. Active dunes.
TBD1	West Thomson Bay dune field. Lat. 59° 05' N., Long. 109° 11' W., elev. 244 m. Active dunes.
TBD2	Central Thomson Bay dune field. Lat. 59° 03' N., Long. 109° 05' W., elev. 270 m. Active

CAD1	East Wolverine dune field. Lat. 59° 07' N., Long. 108° 20' W., elev. 215 m. Beach ridges.
CAD2	West Wolverine dune field. Lat. 59° 08' N., Long. 108° 25' W., elev. 245 m. Active sand
YLD1	Northern Yakow dune field. Lat. 59° 11' N., Long. 108° 10' W., elev. 220 m. Active sand
YLD2	Central Yakow dune field. Lat. 59° 10' N., Long. 108° 00' W., elev. 240 m. Active sand dunes.
	S. alaxensis
NBC1	Summit Lake, B.C. Lat. 58° 38' N., Long. 124° 41' W., elev. 1450 m. Rocky shoreline of lake.
NBC2	Mt. St. Paul, B.C. Lat. 58° 40' N., Long. 124° 46' W., elev. 1540 m. Gravel alluvium.
NBC3	Mile One Thirteen Creek, B.C. Lat. 58° 42' N., Long. 124° 50' W., elev. 1300 m. Creek bed.
NBC4	Trout River, B.C. Lat. 59° 14' N., Long. 125° 50' W., elev. 1200 m. Disturbed creek bed.
NBC5	Toad River, B.C. Lat. 58° 47' N., Long. 125° 34' W., elev. 1290 m. Gravel alluvium.

Data analysis. Levels of allozyme variation were estimated at the species level and for individual populations. Genetic diversity was measured by four parameters: percent polymorphic loci (P), average number of alleles per locus (A), average number of alleles per polymorphic locus (A_P), and expected heterozygosity (H_E). The four diversity parameters were calculated for each population and were averaged across all populations for each species. T-tests were performed to test for significant differences among these population parameters. Species-level statistics were calculated for the four genetic diversity parameters by treating all populations of a species as if they were one population. A locus was considered polymorphic if more than one allele was detected. Fixation indices (F), which reflect deviations of genotypic frequencies from Hardy-Weinberg expectations, were measured as well (Wright, 1922).

The partitioning of genetic diversity within and among populations was analyzed with measures proposed by Nei (1973). The parameter H_T is the total allelic diversity at each polymorphic locus, H_S is the allelic diversity within populations, and D_{ST} is the allelic diversity among populations. The coefficient of gene differentiation (G_{ST}), is the ratio of among population genetic diversity relative to the total genetic diversity. F-statistics (Wright, 1969) elucidated how the detected heterozygosity was structured. The F-statistics include F_{IS}, an index of inbreeding, F_{ST}, an index of reduced heterozygosity due to population subdivision, and F_{IT}, the overall inbreeding coefficient (Wright, 1965). We also calculated Wright's gene flow estimate [Nm_W, where $Nm_W = (1-G_{ST})/4G_{ST}$]. Genetic identities, I, (Nei, 1972) were calculated as well. Population variation statistics (A, A_P, P, and H_E), fixation indices, F-statistics, and standard genetic identities were calculated with the BIOSYS program (Swofford and Selander, 1989). Genetic diversity statistics (H_T, H_S, D_{ST}, and G_{ST}) were calculated with the GENESTAT-PC program (Whitkus, 1988). A

UPGMA phenogram derived from the matrix of the genetic identities was produced using SYSTAT (Wilkinson, 1990).

RESULTS

The 11 enzyme systems assayed in this study are governed by 17 putative loci. Some isozymes were excluded from genetic analysis because they could not be resolved consistently, or had uninterpretable banding patterns (ACP and MNR). The putative loci *G3pdh-1*, *G6pdh-1*, *Got-1*, *Idh-1*, *Lap-2*, *Pgd-1*, and *Pgd-2* were monomorphic in all populations. Ten loci (*G3pdh-2*, *G6pdh-2*, *Gdh-1*, *Got-2*, *Idh-2*, *Lap-1*, *Pgd-3*, *Pgi-1*, *Pgi-2*, and *Skd-1*) were polymorphic in at least some populations (TABLE 4.2). There were 37 alleles at the ten putative polymorphic loci (TABLE 4.2). Alleles unique to a species occurred at frequencies less than 0.50 (TABLE 4.2). *Gdh-1d* was the only allele restricted to populations of *Salix silicicola*, whereas 17 alleles (*G3pdh-2a*, *G6pdh-2b*, *G6pdh-2d*, *G6pdh-2e*, *Gdh-1b*, *Idh-2a*, *Idh-2c*, *Idh-2f*, *Lap-1a*, *Lap-1e*, *Pgd-3a*, *Pgi-1a*, *Pgi-1c*, *Pgi-2a*, *Pgi-2c*, *Skd-1a*, and *Skd1-e*) were restricted to populations of *S. alaxensis*. Overall, *Salix silicicola* differed from *S. alaxensis* by the most common allele at a locus at only two loci (*G6pdh-2* and *Idh-2*; TABLE 4.2).

TABLE 4.2. Allele frequency data for polymorphic loci from eight populations of *Salix silicicola* and five populations of *S. alaxensis*. * indicates alleles unique to *S. alaxensis*, ** indicates the allele unique to *S. silicicola*.

Locus/ allele	*S. silicicola*								*S. alaxensis*				
	WRD1	WRD2	TBD1	TBD2	CAD1	CAD2	YLD1	YLD2	NBC1	NBC2	NBC3	NBC4	NBC5
G3pdh-2													
a*	-	-	-	-	-	-	-	-	0.018	-	-	-	-
b	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.982	1.000	1.000	1.000	1.000
G6pdh-2													
a	0.438	0.288	0.615	0.313	0.476	0.750	0.444	0.719	0.250	0.167	0.333	0.200	0.217
b*	-	-	-	-	-	-	-	-	0.214	0.222	0.333	0.600	0.333
c	0.562	0.712	0.385	0.687	0.524	0.250	0.556	0.281	0.464	0.555	0.334	0.200	0.283
d*	-	-	-	-	-	-	-	-	-	0.056	-	-	0.167
e*	-	-	-	-	-	-	-	-	0.072	-	-	-	-
Gdh-1													
a	0.854	0.769	0.962	0.958	1.000	0.979	0.667	1.000	0.893	0.944	1.000	0.700	0.583
b*	-	-	-	-	-	-	-	-	-	-	-	0.200	0.333
c	-	-	-	0.042	-	-	-	-	0.107	0.056	-	0.100	0.084
d**	0.146	0.231	0.038	-	-	0.021	0.333	-	-	-	-	-	-
Got-2													
a	0.104	0.288	0.135	0.250	0.119	0.125	0.796	0.688	0.375	0.574	0.500	0.200	0.450
b	0.896	0.712	0.885	0.750	0.881	0.875	0.204	0.312	0.625	0.426	0.500	0.800	0.550
Idh-2													
a*	-	-	-	-	-	-	-	-	-	-	0.100	0.300	0.150
b	0.021	-	0.154	-	-	0.063	-	-	0.286	0.259	-	0.300	0.450
c*	-	-	-	-	-	-	-	-	0.286	0.315	0.400	0.100	0.050
d	-	0.212	-	-	0.143	0.145	-	0.188	-	0.185	0.400	0.100	0.050

e	0.979	0.788	0.846	1.000	0.857	0.792	1.000	0.812	0.375	0.185	0.100	0.100	0.100
*f**	-	-	-	-	-	-	-	-	0.053	0.056	-	0.100	0.200
Lap-1													
*a**	-	-	-	-	-	-	-	-	0.393	0.555	0.600	0.300	0.333
b	-	0.058	0.269	-	-	-	-	0.188	0.107	-	-	-	-
c	1.000	0.942	0.731	1.000	1.000	0.979	1.000	0.812	0.393	0.056	0.400	0.700	0.667
d	-	-	-	-	-	0.021	-	-	-	0.389	-	-	-
*e**	-	-	-	-	-	-	-	-	0.107	-	-	-	-
Pgd-3													
*a**	-	-	-	-	-	-	-	-	0.214	0.333	0.200	0.233	0.217
b	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.786	0.667	0.800	0.767	0.783
Pgi-1													
*a**	-	-	-	-	-	-	-	-	0.036	-	-	-	-
b	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.929	1.000	1.000	1.000	1.000
*c**	-	-	-	-	-	-	-	-	0.035	-	-	-	-
Pgi-2													
*a**	-	-	-	-	-	-	-	-	-	0.019	-	-	-
b	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.929	0.981	1.000	0.900	1.000
*c**	-	-	-	-	-	-	-	-	0.071	-	-	0.100	-
Skd-1													
*a**	-	-	-	-	-	-	-	-	0.072	-	0.100	0.200	-
b	-	-	0.037	-	-	-	-	-	-	-	-	0.100	0.050
c	0.250	0.192	0.423	0.271	-	0.146	0.167	0.281	0.071	0.111	-	-	-
d	0.750	0.808	0.538	0.729	1.000	0.854	0.833	0.719	0.857	0.778	0.900	0.700	0.650
*e**	-	-	-	-	-	-	-	-	-	0.111	-	-	0.300

At the species level *Salix silicicola* had considerably less genetic variation than did *S. alaxensis*. Only six loci were polymorphic in *S. silicicola*, whereas in *S. alaxensis*, ten loci were polymorphic. The mean number of alleles per locus, A, (1.59 vs. 2.53), mean number of alleles per polymorphic locus, A_P, (2.67 vs. 3.60), percent polymorphic loci, P, (35.3 vs. 58.9) and average heterozygosity, H_E, (0.108 vs. 0.220) were lower in *S. silicicola* than in *S. alaxensis* (TABLE 4.3). On the average, population level genetic variation was also much lower in *Salix silicicola* than in *S. alaxensis*. Populations of the endemic species had lower mean A (1.30 vs. 1.85), A_P (2.05 vs. 2.85), P (28.7 vs. 45.9) and H_E (0.073 vs. 0.195) than did populations of the presumed progenitor species (TABLE 4.3, all $P < 0.01$).

TABLE 4.3. Summary of allozyme variation for 17 putative loci within eight populations of *Salix silicicola* and five populations of *S. alaxensis*.[1]

Population	N	A	A_P	P	H_E
			S. silicicola		
WRD1	24	1.3	2.0	29.4	0.081
WRD2	26	1.4	2.0	35.3	0.116
TBD1	26	1.4	2.2	35.3	0.116
TBD2	24	1.2	2.0	23.5	0.077
CAD1	21	1.2	2.0	17.6	0.057
CAD2	24	1.4	2.3	35.3	0.076
YLD1	27	1.2	2.0	23.5	0.092
YLD2	32	1.3	2.0	29.4	0.110

Mean	25.5	**1.30	**2.05	**28.7	**0.073
(SE)	1.1	0.04	0.05	2.3	0.022
Species level	204	*1.59	*2.67	35.3	0.108
(SE)	-	0.21	0.21	-	0.041
			S. alaxensis		
NBC1	28	2.1	3.0	58.8	0.215
NBC2	27	1.9	3.2	47.1	0.201
NBC3	30	1.5	2.6	35.3	0.168
NBC4	30	1.9	3.0	47.1	0.212
NBC5	30	1.9	3.3	41.2	0.225
Mean	29.0	**1.85	**2.85	**45.9	**0.195
(SE)	0.7	0.13	0.18	3.9	0.027
Species level	145	*2.53	*3.60	58.9	0.220
(SE)	-	0.42	0.48	-	0.069

[1] N = sample size, A = mean number of alleles per locus, A_P = mean number of alleles per polymorphic locus, P = % polymorphic loci, and H_E = mean expected heterozygosity. * and ** indicate that values differ between species at $P < 0.05$ and $P < 0.01$, respectively.

Fixation indices suggest contrasting levels of inbreeding in the two species. In *Salix silicicola*, 7 of 39 (18%) of the fixation indices are significant and positive, suggesting a deficiency of heterozygotes (TABLE 4.4). In *S. alaxensis*, 14 of 38 (37%) of the *F* values are significant, three positive and 11 negative, suggesting an excess of heterozygotes (TABLE 4.4).

TABLE 4.4. Fixation indices (*F*) for *Salix silicicola* and *S. alaxensis*. [1]

	S. silicicola								*S. alaxensis*				
Locus	WRD1	WRD2	TBD1	TBD2	CAD1	CAD2	YLD1	YLD2	NBC1	NBC2	NBC3	NBC4	NBC5
G3pdh-2	-	-	-	-	-	-	-	-	-0.017	-	-	-	-
G6pdh-2	*0.407	0.224	0.216	0.162	0.236	0.180	-0.169	-0.123	*-0.384	-0.273	-0.500	*-0.429	*-0.210
Gdh-1	0.033	-0.300	-0.067	-0.091	-	-0.032	-0.380	-	-0.120	-0.059	-	*-0.304	*-0.538
Got-2	0.233	-0.031	-0.123	-0.011	-0.143	0.429	-0.125	*0.446	0.067	0.100	0.067	-0.250	0.100
Idh-2	0.395	-0.031	-0.185	-	-0.171	0.317	-	*0.590	*-0.112	-0.433	*-0.515	*-0.250	*-0.351
Lap-1	-	-0.061	*0.439	-	-	-0.015	-	*0.590	*0.566	0.099	0.000	0.167	0.000
Pgd-3	-	-	-	-	-	-	-	-	0.409	0.357	*0.608	*0.418	-
Pgi-1	-	-	-	-	-	-	-	-	-0.057	-	-	-	-
Pgi-2	-	-	-	-	-	-	-	-	-0.037	-0.059	-	0.111	-
Skd-1	*0.556	*0.500	-0.414	0.051	-	-0.132	0.357	-0.205	-0.057	-0.091	-0.111	*-0.304	*-0.443

[1] * indicates that fixation indices differ significantly from Hardy-Weinberg expectations ($P < 0.05$), a dash indicates that loci were monomorphic in the population.

Values obtained for F_{IS} and F_{IT} indicate that, at five of the six polymorphic loci in *S. silicicola*, there is a deficiency of heterozygotes, whereas values obtained for F_{IS} and F_{IT} in *S. alaxensis* indicate that, at seven of the ten polymorphic loci, there is an excess of heterozygotes (TABLE 4.5).

TABLE 4.5. Summary of *F*-statistics for *Salix silicicola* and *S. alaxensis*.

	S. silicicola			*S. alaxensis*		
Locus	F_{IS}	F_{IT}	F_{ST}	F_{IS}	F_{IT}	F_{ST}
G3pdh-2	-	-	-	-0.017	-0.003	0.013
G6pdh-2	0.144	0.326	0.213	-0.355	-0.269	0.064
Gdh-1	-0.201	-0.029	0.144	-0.355	-0.155	0.148
Got-2	0.112	0.271	0.179	0.036	0.098	0.064
Idh-2	0.175	0.270	0.114	-0.281	-0.138	0.112
Lap-1	0.413	0.503	0.154	0.192	0.304	0.138
Pgd-3	-	-	-	0.437	0.480	0.075
Pgi-1	-	-	-	-0.057	-0.011	0.043
Pgi-2	-	-	-	-0.081	-0.031	0.046
Skd-1	0.048	0.134	0.091	-0.274	-0.139	0.106
Mean	0.101	0.241	0.156	-0.116	-0.007	0.098

Total genetic diversity at polymorphic loci (H_T) in *Salix silicicola* was 0.305, compared to 0.384 in *S. alaxensis* (TABLE 4.6). The among-population differentiation (G_{ST}) was higher in the endemic (0.159) than it was in the presumed progenitor (0.097). Estimates of gene flow were moderate in both species. Wright's estimate (Nm_W) for *Salix silicicola* was 1.32 migrants per generation and for *S. alaxensis* it was 2.33 migrants per generation (TABLE 4.6).

TABLE 4.6. Genetic diversity statistics (Nei, 1973), and estimates of gene flow *for Salix silicicola* and *S. alaxensis*. Genetic diversity parameters were calculated for polymorphic loci only.[1]

Species	No. of Loci	H_T	H_S	D_{ST}	G_{ST}	Nm_W
S. silicicola	6	0.305	0.256	0.048	0.159	1.32
S. alaxensis	10	0.384	0.347	0.037	0.097	2.33

[1] H_T = total gene diversity, H_S = gene diversity within populations, D_{ST} = gene diversity among populations, G_{ST} = the proportion of gene diversity apportioned among populations, and Nm_W = Wright's gene flow estimate.

Genetic identity values (*I*) for all pairs of populations were high. Intraspecific *I* values for populations of *Salix silicicola* ranged from 0.954 to 0.998 with a mean of 0.981; for *S. alaxensis*, *I* values ranged from 0.947 to 0.987 with a mean of 0.973. The mean of genetic identity values between *S. silicicola* and *S. alaxensis* was 0.932, and ranged from 0.902 to 0.963. A UPGMA cluster analysis based on genetic identity values depicts the close genetic relationship among populations of each species and a more distant genetic relationship among populations of the two species (FIGURE 4.2).

DISCUSSION

Genetic Diversity. The plant allozyme literature indicates that the values of several population genetic parameters are correlated with narrow endemism (Karron, 1987; Hamrick and Godt, 1989; Hamrick et al., 1991). Species with restricted geographic distributions generally have fewer polymorphic loci, fewer alleles per locus, and reduced heterozygosity (Gottlieb, 1973; Karron et al., 1988; Loveless and Hamrick, 1988; Pleasants and Wendel, 1989; Bayer, 1992; Sherman-Broyles et al., 1992; Purdy Bayer, and Macdonald, 1994 [chapter 2]) when compared to widespread congeners.

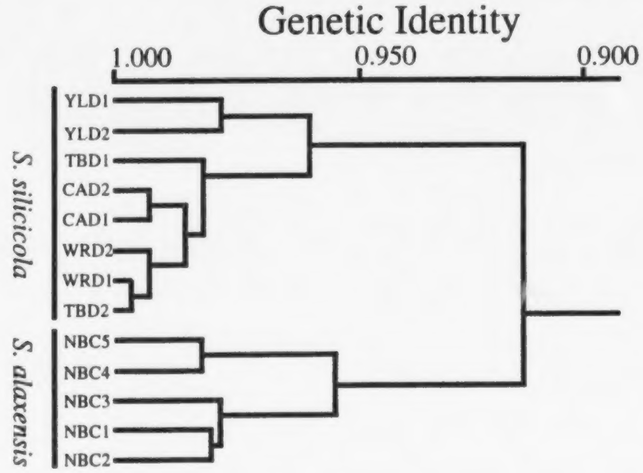

Fig 4.2. UPGMA cluster analysis of eight populations of *Salix silicicola* and five populations of *S. alaxensis* based on Nei's (1972) measure of genetic identity (*I*). The cophenetic correlation coefficient was 0.892.

The results of this study are consistent with previous investigations on genetic diversity in endemic taxa. *Salix silicicola* has considerably less species-level and population-level genetic variation than does its widespread presumed progenitor, *S. alaxensis*. The mean number of alleles per locus, mean number of alleles per polymorphic locus, percent polymorphic loci, and heterozygosity were all lower in the endemic taxon. Allozyme studies on other Athabasca sand dune endemics (Purdy, Bayer, and Macdonald, 1994 [chapter 2]; Purdy and Bayer, 1995 [chapter 3]) have found endemic taxa to have less genetic variation than do their related widespread progenitor taxa, though the relationship between the progenitor and derivative species differ from the present study.

Deschampsia mackenzieana is a reproductively isolated, tetraploid endemic that occurs in sympatry with its diploid progenitor, *D. cespitosa*. A genetic bottleneck at the time of origin during polyploidization was thought to be the factor responsible for the significantly lower genetic diversity in *D. mackenzieana* (Purdy and Bayer, 1995 [chapter 3]). Although *Stellaria arenicola* had less genetic diversity than *S. longipes*, sympatric populations of the progenitor were thought to provide additional genetic variation through interspecific gene flow because the two taxa are sympatric and hybridize in a number of locations on the Athabasca sand dunes (Purdy, Bayer, and Macdonald, 1994 [chapter 2]).

Mean values compiled from Hamrick and Godt (1989) for A (1.39), P (26.3), and H_E (0.063) in endemic taxa resembled those found in *Salix silicicola* ($A = 1.30$; $P = 28.7$; and $H_E = 0.073$). Values for the same parameters in widespread plant taxa ($A = 1.72$; $P = 43.0$; and $H_E = 0.159$), taxa with animal-outcrossed breeding system ($A = 1.54$; $P = 35.9$; and $H_E = 0.124$), or wind-dispersed seeds ($A = 1.70$; $P = 42.9$; and $H_E = 0.123$), resembled those for *S. alaxensis* ($A = 1.85$; $P = 45.9$; and $H_E = 0.195$).

In the only other study of allozyme variation in the genus, Brunsfeld, Soltis, and Soltis (1991) generally found that widespread *Salix* species of the section Longifoliae had the highest mean values for A, P, and H_E. Although levels of population genetic variation in *S. exigua* and *S. interior* (Brunsfeld, Soltis, and Soltis, 1991), two geographically widespread species, were high and resembled the values obtained for *S. alaxensis* in this study, *S. silicicola*, had less population genetic variation than did *S. fluviatilis* and *S. sessifolia*, two species with narrow geographic ranges. Other factors, such as the evolutionary nature of populations at the margin of their range or species with small population sizes but extensive distributions (e.g., *S. taxifolia*) affected levels of genetic variation (Brunsfeld, Soltis, and Soltis, 1991). Factors that promote high levels of genetic diversity within populations in *Salix* species include dioecism, high fecundity, wind-dispersed seeds and long-lived clonal growth (Hamrick and Godt, 1989).

Although *Salix silicicola* lacks much of the genetic variation found in *S. alaxensis*, its genetic diversity was high at polymorphic loci ($H_T = 0.305$). The G_{ST} values indicate that most of the genetic diversity occurs within populations for both species (TABLE 4.6), although G_{ST} values were higher in *S. silicicola*. Gene flow estimates based on G_{ST} values were moderate for both species, which is consistent with the outcrossed dioecious breeding system and wind-dispersed seeds characteristic of *Salix* species. The low amount of among population differentiation is reflected in the high intraspecific genetic identity values obtained.

At individual loci, there was an excess of heterozygotes over that expected under random mating in *Salix alaxensis*, but a deficiency of heterozygotes in *S. silicicola* (TABLE 5). The value of F_{IS} was -0.116 in *S. alaxensis*, indicating an 11.6% excess of heterozygotes, relative to Hardy-Weinberg expectations. Heterozygosity may confer a fitness advantage, or provide physiological plasticity in fluctuating environments (Huenneke, 1991). Levels of heterozygosity are positively correlated with radial growth in *Populus tremuloides* Michx. (Mitton and Grant, 1980), a member of the Salicaceae.

Although the levels of heterozygosity in *Salix alaxensis* were higher than expected, departures from Hardy-Weinberg equilibrium values on a locus by locus basis were not consistent. An absence of any strong singular pattern in F-statistics for *S. alaxensis* suggests several forces are probably acting, which differentially affect loci in the populations. There is a consistent deficiency of heterozygotes in *S. silicicola* at five of the six polymorphic loci. The F_{IS} values indicate that there was a 10.1% deficiency of heterozygotes relative to Hardy-Weinberg expectations. The difference in F_{IS} values between *S. alaxensis* and *S. silicicola* may suggest heterosis is not a force acting upon the endemic *S. silicicola* populations, or that directional selection is still occurring at other loci linked with the isozyme loci investigated here. Alternatively, the observed deficit of heterozygotes in *S. silicicola* may be caused by the Wahlund effect, or by biparental inbreeding.

Origin of Salix silicicola. Several predictions have been made concerning the relationship between progenitor and derivative taxa (Gottlieb, 1973; Pleasants and Wendel, 1989); all of them were met in this study. First, the allelic diversity of *Salix silicicola* was a subset of the gene pool of *S. alaxensis*, and it included only one unique allele. Second, there was less genetic variation in *S. silicicola* than was found in *S. alaxensis*. Third, the intraspecific genetic identities among populations of *S. silicicola* resembled the interspecific genetic identities with populations of *S. alaxensis*. These three expectations concerning the genetic relationship between progenitor-derivative species pairs were met in other studies of endemics from the Athabasca sand dunes (Purdy, Bayer, and Macdonald, 1994 [chapter 2]; Purdy and Bayer, 1995 [chapter 3]).

Mean intraspecific genetic identities for *Salix* species in the section Longifoliae ranged from 0.987 for *S. fluviatilis* to 0.875 for *S. melanopsis* (Brunsfeld, Soltis, and Soltis, 1991). Mean intraspecific *I* values for *S. silicicola* and *S. alaxensis* were 0.981 and 0.973 respectively, values which fall within the range of values reported for other *Salix* species. Mean interspecific *I* values for *Salix* species in the section Longifoliae ranged from 0.580 to 0.961 (Brunsfeld, Soltis, and Soltis, 1991), although most values were less than 0.900. Interspecific genetic identities between populations of *S. silicicola* and *S. alaxensis* were high compared to those values (mean = 0.932; range = 0.902 to 0.963). The high genetic identities suggest a recent origin for the endemic *S. silicicola*. Other recent progenitor-derivative species pairs exhibit similar values (Gottlieb, 1973; Crawford and Smith, 1982a, 1982b; Crawford, Ornduff, and Vasey, 1985; Gottlieb, Warwick, and Ford, 1985; Loveless and Hamrick, 1988; Purdy, Bayer, and Macdonald, 1994 [chapter 2]; Purdy and Bayer, 1995 [chapter 3]).

The Athabasca sand dune endemic taxa are believed to have evolved after the sand dunes were formed following the Pleistocene, 8,000 years ago (Raup and Argus, 1982). The ecology, population genetics, and systematics of Athabasca sand dune endemics that are sympatric with their progenitor species have been the subject of previous investigations (Argus and Steele, 1979; Macdonald et al., 1987; Purdy, Bayer and Macdonald, 1994 [chapter 2]; Purdy and Bayer, 1995 [chapter 3]). However, populations of *Salix alaxensis*, the presumed progenitor taxon of *S. silicicola*, occur near to and above treeline in the Northwest Territories, 300 km north of the dunes (Porsild and Cody, 1980). Putative allopatric progenitor populations of two other Athabasca sand dune endemic taxa also derived from arctic ancestors, *Armeria maritima* subsp. *interior* (Raup) Porsild and *Silene acaulis* f. *athabascensis* Argus, are found in the same region (Argus and Steele, 1979).

Salix silicicola differs from *S. alaxensis* by its very dense and persistent vestiture that covers the leaves and branches (Raup, 1959). Tomentose plants of *S. alaxensis* have been collected only from Pelly Lake, in the district of Keewatin, N.W.T. (Argus and Steele, 1979). This is the same location where populations of *S. planifolia* subsp. *planifolia* Pursh, the progenitor of another sand dune endemic willow, *S. planifolia* subsp. *tyrrellii* (Raup) Argus, occur. Argus and Steele (1979) speculated that relics of these arctic gene pools became isolated in the active sand dunes during the thermal maximum about 5000 years B.P.

Because isozyme data from populations of *Salix alaxensis* from the Keewatin are not available, we do not know how much genetic variation occurs in the populations thought to have been the progenitor gene pool for *S. silicicola*. Populations of *S. alaxensis* from northern British Columbia examined in this study maintain much higher amounts of genetic variation than do *S. silicicola*. Theoretical and empirical evidence suggest that genetic bottlenecks have a large effect on allelic diversity and also affect heterozygosity (Wright, 1931; Nei, Maruyama, and Chakraborty, 1975; Leberg, 1992). Populations of *S. silicicola* from different dune fields are genetically similar in terms of their genetic identities, which suggests either that significant genetic drift has not occurred since the endemic became abundant or that gene flow is occurring among populations. We hypothesize that founding populations of the endemic were small, and that ensuing genetic bottlenecks and strong directional selection for sand dune adapted traits caused the observed reduction of genetic diversity in the endemic. It would be of interest to investigate the population genetics of *S. alaxensis* and other progenitor taxa from the Keewatin district of the Northwest Territories to test whether this region is, in fact, the relictual progenitor gene pool for several endemic taxa from the Athabasca sand dunes.

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Chapter Five

Genetic variation in the endemic *Achillea millefolium* subsp. *megacephala* (Asteraceae) from the Athabasca sand dunes and the widespread *A. millefolium* subsp. *lanulosa* in western North America [1]

ABSTRACT. A comprehensive analysis of genetic diversity in endemic plant taxa of the Athabasca sand dunes in northern Saskatchewan, Canada, is now underway. In this study, genetic variation was examined by starch gel electrophoresis in six populations of *Achillea millefolium* subsp. *megacephala*, an endemic of the Athabasca sand dunes, and 13 populations of the closely related widespread taxon, *Achillea millefolium* subsp. *lanulosa*. Thirty-five alleles were detected at nine polymorphic loci though only 28 alleles had a frequency greater than 0.05 in any one population. Six alleles were restricted to the endemic taxon whereas twelve alleles were restricted to populations of the progenitor. Populations of the endemic had more alleles per locus (1.45 vs. 1.31), higher percent polymorphic loci (31.6 vs. 23.1) and greater genetic diversity (0.126 vs. 0.085) than did populations of the widespread taxon. Genetic identities within species averaged 0.988 for *Achillea millefolium* subsp. *megacephala* and 0.961 for *Achillea millefolium* subsp. *lanulosa* and between species identities ranged from 0.874 to 0.993 with a mean of 0.943. At polymorphic loci, total gene diversity was comparable in both taxa (*Achillea millefolium* subsp. *megacephala*, $H_T = 0.296$; *Achillea millefolium* subsp. *lanulosa*, $H_T = 0.254$) though within population gene diversity was considerably higher in the endemic ($H_S = 0.272$) than in the widespread taxon ($H_S = 0.178$). Population differentiation was considerably lower in *Achillea millefolium* subsp. *megacephala* ($G_{ST} = 0.078$) than in *Achillea millefolium* subsp. *lanulosa* ($G_{ST} = 0.300$), though G_{ST} values were reduced when the parameter was calculated separately for geographic subdivisions of the progenitor. Our results differ from previous studies in which the endemic is typically depauperate of genetic variation relative to related widespread species. We suggest that forced sexual reproduction and the absence of long-term asexual reproduction may be one of a number of factors that help populations of *Achillea millefolium* subsp. *megacephala* maintain higher levels of genetic variation on the Athabasca sand dunes.

INTRODUCTION

Widespread species of plants must adapt to a broad range of environmental conditions in order to maintain their large geographic distributions. Consequently, to exist in such an extensive range of habitats, many widespread species have high genetic diversity (Hamrick and Godt, 1989), and have evolved into a series of ecological races (Turesson, 1922), or exhibit considerable phenotypic plasticity (Schlichting, 1986). The experiments of Clausen, Keck, and Hiesey (1940) were the first to comprehensively demonstrate the importance of both genetic differentiation and phenotypic plasticity for plant species to adapt to and survive in a wide range of environmental conditions. Endemics, which are often restricted to a much narrower range of environmental conditions, do not have the same requirement for considerable genetic diversity, population differentiation, or phenotypic plasticity for survival.

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Studies comparing closely related widespread and endemic species have shown that endemic species generally have less genetic diversity (McLeod et al., 1983; Gottlieb, Warwick, and Ford, 1985; Karron, 1987; Karron et al. , 1988; Loveless and Hamrick, 1988; Moran, Muona, and Bell, 1989; Pleasants and Wendel, 1989; Hamrick and Godt, 1989; Soltis and Soltis, 1991; Baskauf, McCauley, and Eickmeier, 1994; Purdy, Bayer, and Macdonald, 1994 [chapter 2]; Purdy and Bayer, 1995a [chapter 3], 1995b [chapter 4]). Whether low levels of genetic variation in endemic species are a cause or consequence of a restricted geographic distribution is still the subject of debate (Huenneke, 1991). While various historical, ecological, and genetic hypotheses have been presented as to the causes of rarity (Stebbins, 1980; Kruckeberg and Rabinowitz, 1985), no single explanation can be applied to all species.

Achillea millefolium subsp. megacephala

The members of the *Achillea millefolium* L. complex occur in many habitats of the temperate and subarctic regions of the northern hemisphere (Clausen, Keck, and Hiesey, 1948). In occupying such a diversity of environments, this complex has evolved a variety of ecological races adapted to specific environmental conditions. Variation in the species is attributable to genetic differentiation, phenotypic plasticity, and polyploidy (Clausen, Keck, and Hiesey, 1940, 1948; Warwick and Briggs, 1980; Warwick and Black, 1982). Presently, there is no satisfactory taxonomic treatment of the variation within the *A. millefolium* complex in North America (Warwick and Black, 1982). Typically, two variants of *A. millefolium* are recognized in the boreal forest of North America, *lanulosa* and *borealis*, which have been variously treated as unique species, or subspecies and varieties of *A. millefoilium* (Kartesz and Kartesz, 1980).

On the south shore of Lake Athabasca in northwestern Saskatchewan, there is a unique assemblage of sand dune-adapted endemic plant taxa (Raup, 1936; Raup and Argus, 1982). The flora of the Athabasca sand dunes is notable because endemic taxa are rare in boreal and arctic regions (Kruckeberg and Rabinowitz, 1985). There are populations of the *lanulosa* variant, *Achillea millefolium* subsp. *megacephala* (Raup) Argus, that have adapted to the shifting sand dune environment characteristic of the region. The endemic *A. millefolium* subsp. *megacephala* differs from other northern races of *A. millefolium* subsp. *lanulosa* (Nutt.) Piper in having a large involucre, and in having considerable pubescence on stems and leaves. Though the taxonomy of the group as a whole is not well understood, *A. millefolium* subsp. *megacephala* is at least a distinct ecotype and shares characters common in other endemics that are considered adapted to the open sand dune environment of the Athabasca sand dunes, such as increased pubescence (Argus and Steele, 1979). *Achillea millefolium* subsp. *megacephala* is a rare endemic of the Athabasca sand dunes and is found only on the William River and Thomson Bay dune fields (FIGURE 5.1).

This study was initiated to investigate the genetic diversity within and among populations of the rare *Achillea millefolium* subsp. *megacephala*. We were interested in comparing levels of genetic diversity in this endemic with populations of *A. millefolium* found in other habitats of western North America. We hypothesized that the amount of genetic diversity within and among populations of *A. millefolium* from the Athabasca sand dunes would not necessarily be different from that found in other races of the species, since *A. millefolium* has demonstrated the capacity to evolve ecological races adapted to a wide variety of habitats in temperate and subarctic regions. Also, since we have begun to collect information on the genetic structure of populations of other Athabasca sand dune endemic plant species, these data provide additional information into the origin of the unique flora of the region.

MATERIALS AND METHODS

Population sampling The locations of the populations that were sampled for this study are found in FIGURE 5.1 and TABLE 5.1. Populations of *Achillea millefolium* subsp.

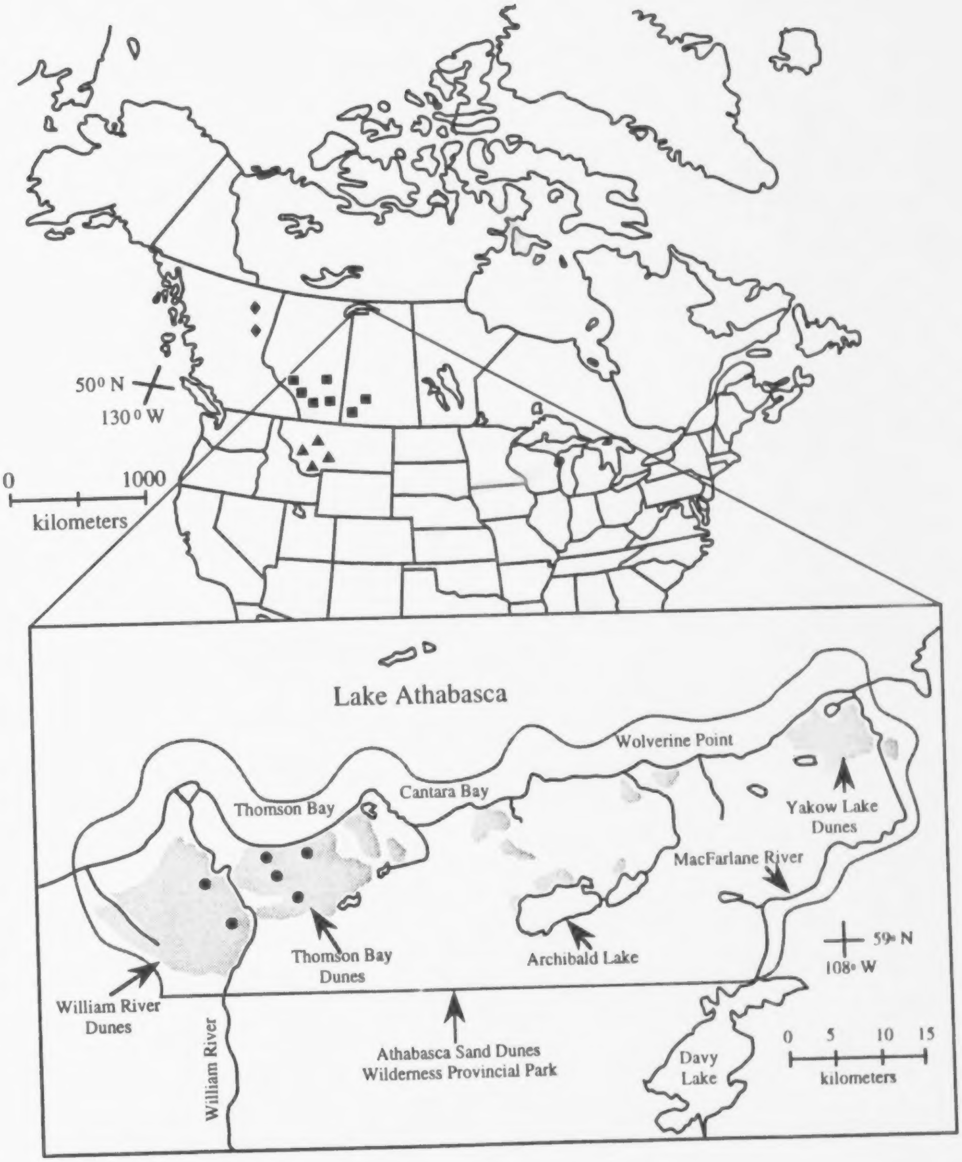

FIGURE 5.1. Locations of populations sampled in this study of the widespread *Achillea millefolium* subsp. *lanulosa* from northern (diamonds), central (squares), and southern (triangles) regions and the Athabasca sand dune endemic *A. millefolium* subsp. *megacephala* (circles).

lanulosa were sampled widely through western North America, whereas populations of *A. millefolium* subsp. *megacephala* were collected from throughout their range on the Athabasca sand dunes (FIGURE 5.1). The number of populations and individuals, respectively, examined for each subspecies were: *A. millefolium* subsp. *megacephala* (6, 127) and *A. millefolium* subsp. *lanulosa* (13, 310). The number of populations and individuals collected for *A. millefolium* subsp. *lanulosa* from different geographic regions were: north (2, 45), central (7,149), and south (4, 116).

Live plants which included leaves and below ground rhizomes were collected from up to 50 individuals in each population. To ensure the collection of distinct genets, we generally collected individuals that were greater than 3 meters apart. The collections were transported, wrapped in live *Sphagnum* and in coolers, to the phytotron at the University of Alberta, where the live plants were grown in soil in Spencer-Lemaire containers.

Electrophoresis. Standard methods for starch gel electrophoresis were employed in this study (Soltis et al., 1983; Purdy, Bayer, and Macdonald, 1994 [chapter 2]). Fresh pieces of actively growing leaf tissue were ground in cold extraction buffer. The supernatant was absorbed onto filter paper wicks, frozen at -20° C overnight, and electrophoresed the following morning. The filter paper wicks were loaded onto 12% starch gels.

TABLE 5.1. Population designation, collection location, habitat, and sample size for populations of *Achillea millefolium* subsp. *lanulosa* (north, central, and south) and *A. lanulosa* subsp. *megacephala* (dunes) sampled in this study.

Pop.	Population location and habitat.
	Dunes
ASD1	Central William River dune field. Lat. 59° 03’ N., Long. 109° 20’ W., elev. 244 m. Active sand dunes.
ASD2	South William River dune field. Lat. 58° 55’ N., Long. 109° 12’ W., elev. 275 m. Active sand dunes.
ASD3	West Thomson Bay dune field. Lat. 59° 05’ N., Long. 109° 11’ W., elev. 244 m. Active sand dunes.
ASD4	East Thomson Bay dune field. Lat. 59° 06’ N., Long. 108° 59’ W., elev. 270 m. Active rolling dunes.
ASD5	Central Thomson Bay dune field. Lat. 59° 03’ N., Long. 109° 05’ W., elev. 270 m. Active sand dunes.
ASD6	Thomson Bay shoreline. Lat. 59° 05’ N., Lat. 109° 10’ W., elev. 215 m. Disturbed beach ridges.
	North
BC1	Buckinghorse River, B.C. Lat. 57° 25’ N., Long. 122° 50’ W., elev. 1,010 m. Gravel floodplain.
BC2	Toad River, B.C. Lat. 59° 10’ N, Long. 125° 50’ W, elev. 855 m. Gravel floodplain.
	Central
AB1	Gooseberry Lake, Alberta. Lat. 52° 45’ N, Long. 110° 50’ W, elev. 645 m. Wet parkland meadow.
AB2	Battle River, Alberta. Lat. 52° 53’ N, Long. 111° 02’ W, elev. 610 m. Mixed grassland.
AB3	Ram Mountain, Alberta. Lat. 52° 20’ N, Long. 115° 45’ W, elev. 1,860 m. Open subalpine forest.
AB4	Red Deer River, Alberta. Lat. 50° 55’ N, Long. 111° 53’ W, elev. 646 m. Riparian habitat.
AB5	Waiperous Creek, Alberta. Lat. 51° 25’ N, Long. 115° 05’ W, elev. 1,500 m. Gravel floodplain.
SK1	Webb, Saskatchewan. Lat. 50° 18’ N, Long. 108° 13’ W, elev. 735 m. Moist prairie.

SK2	Antelope Lake, Saskatchewan. Lat. 50° 17' N, Long. 108° 24' W, elev. 701 m. Moist prairie.
	South
MT1	Highwood Mountains, Montana. Lat. 47° 30' N, Long. 110° 32' W, 1,372 m. Pine forest.
MT2	Crazy Mountains, Montana. Lat. 46° 18' N, Long. 110° 25' W, elev. 1,830 m. Pine forest.
MT3	Branham Lake, Montana. Lat. 45° 30' N, Long. 112° 00' W, elev. 2,680 m. Subalpine meadow.
MT4	Echo Lake, Montana. Lat. 46° 14' N, Long. 113° 15' W, elev. 2,012 m. Wet willow community.

Three buffer systems were used to resolve the isozymes in this study (Purdy, Bayer, and Macdonald, 1994 [chapter 2]). Fifteen enzyme systems were resolved. Leucine aminopeptidase (LAP), phosphoglucose isomerase (PGI), aldolase (ALD), aconitase (ACO), and glutamate oxalate-transaminase (GOT) were resolved on system I. Menadione reductase (MNR), glucose-6-phosphate dehydrogenase (G6PDH), isocitrate dehydrogenase (IDH), shikimic acid dehydrogenase (SKD), and acid phosphatase (ACP) were resolved on system II. 6-phosphogluconate (PGD), malate dehydrogenase ([NADP]ME), malate dehydrogenase ([NAD]MDH), phosphoglucose mutase (PGM), and glyceraldehyde-3-phosphate dehydrogenase (G3PDH) were resolved on system III.

Enzymatic assays followed Soltis et al. (1983), except for MNR (Wendel and Weeden, 1989). For enzymes with more than one putative locus, the staining zones were numbered sequentially, with the most anodally migrating isozyme designated as 1, the next 2, and so on. Similarly, the most anodal allozyme of a gene was labeled A, etc. Bands were categorized as isozymes and allozymes by observing segregation of bands among individuals in the populations sampled in light of the typical subunit structure and subcellular compartmentalization (Gottlieb, 1981; Weeden and Wendel, 1989). Allele frequencies at each locus were determined for each population.

Genetic analysis. To provide a measure of the level of genetic variation within populations and subspecies, the following statistics were computed: A, the mean number of alleles per locus; A_P, the mean number of alleles per polymorphic locus; P, the proportion of polymorphic loci when the most common allele has a frequency less than or equal to 0.95; and H_E, the expected panmictic heterozygosity. Values for A, A_P, P, and H_E were calculated for each population, which were then averaged for each subspecies or geographic region. Sub-species level statistics were calculated for the four genetic diversity parameters by treating all populations of a taxon as if they were one population. T-tests were used to test for significant differences among these population parameters when only two comparisons could be made, whereas ANOVA followed by Student-Newman-Keuls multiple range tests was employed when more than one comparison was to be made for a given population parameter. The partitioning of genetic diversity within and among populations was analyzed using measures proposed by Nei (1973). We also calculated Wright's (1951) gene flow estimate and genetic identities (Nei, 1978).

Population variation statistics and standard genetic identities were calculated using the BIOSYS program (Swofford and Selander, 1989). Genetic diversity statistics were calculated using the GENESTAT-PC program (Whitkus, 1988). Principal components analysis (PCA) using the SYSTAT program (Wilkinson, 1990) helped evaluate the phenetic interpopulational relationships based on allele frequency distributions from polymorphic loci only.

RESULTS

The 15 enzyme systems assayed in this study are coded by 19 putative loci. Some isozymes (ALD, MNR, ME, ACP-2, ACP-3) were excluded from our analysis because they had complex banding patterns, were resolved inconsistently, or overlapped with other loci. Ten of the loci were monomorphic in all populations: *Aco-1*, *Acp-1*, *G3pdh-1*, *G6pdh-1*, *G6pdh-2*, *Lap-1*, *Mdh-1*, *Mdh-2*, *Pgi-1*, and *Pgm-1*. Nine of the loci were polymorphic in at least some populations: *Got-1*, *Idh-1*, *Idh-2*, *Lap-2*, *Mdh-3*, *Pgd-1*, *Pgi-2*, *Pgm-2*, and *Skd-1*. Allele frequencies for polymorphic loci for all populations are presented in TABLE 5.2.

TABLE 5.2. Allele frequency data for polymorphic loci from populations of *Achillea millefolium* subsp. *lanulosa* (north, central, and south) and subsp. *megacephala* (dunes). * indicates alleles unique to the endemic, whereas ** indicates alleles unique to the progenitor taxon.

Locus/	Dunes						North	
allele	ASD1	ASD2	ASD3	ASD4	ASD5	ASD6	BC1	BC2
Got-1								
a*	0.312	0.571	0.227	0.152	0.250	0.278	-	-
b**	-	-	-	-	-	-	0.158	0.071
c	0.688	0.429	0.773	0.848	0.750	0.722	0.842	0.929
d**	-	-	-	-	-	-	-	-
Idh-1								
a**	-	-	-	-	-	-	-	-
b**	-	-	-	-	-	-	0.559	0.500
c	1.000	1.000	1.000	1.000	1.000	1.000	0.441	0.500
Idh-2								
a*	0.104	0.036	0.045	0.104	0.545	0.147	-	-
b	0.896	0.964	0.955	0.896	0.432	0.853	0.531	0.571
c	-	-	-	-	0.023	-	0.469	0.429

d**	-	-	-	-	-	-	-	-
Lap-2								
a**	-	-	-	-	-	-	-	-
b	0.729	0.615	0.444	0.652	0.400	0.400	0.722	0.750
c	0.271	0.385	0.556	0.348	0.600	0.600	0.278	0.250
Mdh-3								
a	0.021	-	0.273	0.125	0.250	0.278	-	-
b**	-	-	-	-	-	-	-	-
c	0.979	1.000	0.727	0.833	0.750	0.722	1.000	1.000
d*	-	-	-	0.042	-	-	-	-
Pgd-1								
a	0.042	0.036	0.273	0.091	0.250	0.167	0.132	0.107
b	0.958	0.964	0.727	0.909	0.750	0.805	0.868	0.893
c*	-	-	-	-	-	0.028	-	-
Pgi-2								
a*	0.193	0.214	0.167	0.167	0.045	0.324	-	-
b**	-	-	-	-	-	-	0.079	-
c	0.019	-	-	-	-	-	-	-
d	-	-	0.167	0.041	0.045	0.088	-	-
e	0.788	0.786	0.666	0.792	0.910	0.588	0.921	1.000
f**	-	-	-	-	-	-	-	-
Pgm-2								
a**	-	-	-	-	-	-	-	-
b	0.542	0.615	0.818	0.568	0.738	0.500	0.306	0.036
c	0.458	0.385	0.182	0.432	0.190	0.500	0.694	0.964
d	-	-	-	-	0.072	-	-	-
e**	-	-	-	-	-	-	-	-
Skd-1								
a	0.958	1.000	1.000	1.000	0.977	1.000	1.000	1.000
b*	0.042	-	-	-	0.023	-	-	-
c**	-	-	-	-	-	-	-	-

TABLE 5.2. continued.

Locus/	Central							South			
allele	AB1	AB2	AB3	AB4	AB5	SK1	SK2	MT1	MT2	MT3	MT4
Got-1											
a*	-	-	-	-	-	-	-	-	-	-	-
b**	-	-	-	-	-	-	-	-	-	-	-
c	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.981
d**	-	-	-	-	-	-	-	-	-	-	0.019
Idh-1											
a**	-	-	-	-	-	-	-	-	-	0.238	-
b**	0.400	0.308	0.469	0.458	0.083	0.361	0.136	0.297	0.391	0.167	0.542
c	0.600	0.692	0.531	0.542	0.917	0.639	0.864	0.703	0.609	0.595	0.458
Idh-2											
a*	-	-	-	-	-	-	-	-	-	-	-
b	0.893	0.654	0.850	0.667	0.917	0.889	0.881	0.984	0.860	1.000	0.885
c	-	-	-	-	-	-	-	-	-	-	-
d**	0.107	0.346	0.150	0.333	0.083	0.111	0.119	0.016	0.140	-	0.115
Lap-2											
a**	-	-	-	-	0.100	-	-	-	-	-	-
b	1.000	1.000	1.000	1.000	0.650	1.000	0.826	0.845	0.880	0.808	0.860
c	-	-	-	-	0.250	-	0.174	0.155	0.120	0.192	0.140
Mdh-3											

a	-	-	-	0.375	0.042	-	-	-	-	-	-
*b***	-	-	-	-	-	-	-	0.094	0.281	-	-
c	1.000	1.000	1.000	0.625	0.958	1.000	1.000	0.906	0.719	1.000	1.000
*d**	-	-	-	-	-	-	-	-	-	-	-
Pgd-1											
a	-	-	-	-	-	-	0.083	-	-	-	-
b	1.000	1.000	1.000	1.000	1.000	1.000	0.917	1.000	1.000	1.000	1.000
*c**	-	-	-	-	-	-	-	-	-	-	-
Pgi-2											
*a**	-	-	-	-	-	-	-	-	-	-	-
*b***	-	-	-	-	0.042	-	-	0.031	0.015	0.038	0.019
c	-	-	-	1.000	0.208	-	0.104	0.125	0.047	-	-
d	-	-	-	-	-	-	-	0.844	0.938	0.962	0.962
e	1.000	1.000	1.000	-	0.750	1.000	0.896	-	-	-	-
*f***	-	-	-	-	-	-	-	-	-	-	0.019
Pgm-2											
*a***	-	-	-	-	-	-	-	-	-	-	0.022
b	0.278	0.409	0.406	0.333	0.292	0.406	0.042	0.214	0.367	0.229	0.086
c	0.722	0.591	0.500	0.667	0.708	0.563	0.958	0.750	0.633	0.771	0.783
d	-	-	0.063	-	-	0.031	-	0.036	-	-	0.109
*e***	-	-	0.031	-	-	-	-	-	-	-	-
Skd-1											
a	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.984	1.000	1.000	0.942
*b**	-	-	-	-	-	-	-	-	-	-	-
*c***	-	-	-	-	-	-	-	0.016	-	-	0.058

There were 35 alleles at the nine polymorphic loci, though only 28 alleles had frequencies greater than 0.05 in any one population (TABLE 5.2). Six alleles were restricted to the endemic taxon (*Got-1a*, *Idh-2a*, *Mdh-3d*, *Pgd-1c*, *Pgi-2a*, and *Skd-1b*), though three of these never occurred at frequencies greater than 0.05 (*Mdh-3d*, *Pgd-1c*, and *Skd-1b*). Twelve alleles were restricted to the widespread taxon (*Got-1b*, *Got-1d*, *Idh-1a*, *Idh-1b*, *Idh-2d*, *Lap-2a*, *Mdh-3b*, *Pgi-2b*, *Pgi-2f*, *Pgm-2a*, *Pgm-2e*, and *Skd-1c*), though four of these alleles never occurred at frequencies greater than 0.05 (*Got-1d*, *Pgi-2f*, *Pgm-2a*, and *Pgm-2e*).

At the population level, *Achillea millefolium* subsp. *megacephala* had more genetic variation than *A. millefolium* subsp. *lanulosa* (TABLE 5.3). Mean values for A (1.45 vs. 1.31), A_P (2.21 vs. 2.16), P (31.6 vs. 23.1), and H_E (0.126 vs. 0.085) were all higher in *A. millefolium* subsp. *megacephala* compared to *A. millefolium* subsp. *lanulosa*. Subdividing *A. millefolium* subsp. *lanulosa* into different geographic regions indicates central and northern populations generally have less genetic variation than southern populations (TABLE 5.3). In contrast, at the sub-species level, where all populations of a taxon were considered as if they were one population, *A. millefolium* subsp. *lanulosa* has slightly higher genetic diversity for A, A_P, and P, than *A. millefolium* subsp. *megacephala*, though the overall heterozygosity (H_E) is still lower for *A. millefolium* subsp. *lanulosa* (TABLE 5.3).

TABLE 5.3. Summary of allozyme variation for 19 loci within populations of *Achillea millefolium* subsp. *lanulosa* from different geographic regions and the endemic subsp. *megacephala* (dunes). [1]

Population	N	A	A_P	P	H_E	H_O
			Dunes			
ASD1	23	1.47	2.13	26.3	0.123	0.110
ASD2	27	1.32	2.00	21.1	0.114	0.102
ASD3	12	1.42	2.14	31.6	0.115	0.139
ASD4	24	1.47	2.29	36.8	0.112	0.118
ASD5	22	1.58	2.38	36.8	0.122	0.148
ASD6	18	1.47	2.29	36.8	0.167	0.157
Mean		1.45	2.21	31.6	0.126	0.129
(SE)		0.03	0.06	2.7	0.008	0.009
			North			
BC1	19	1.37	2.00	36.8	0.110	0.133
BC2	20	1.32	2.00	26.3	0.079	0.096
Mean		1.34	2.00	31.6	0.095	0.115
(SE)		0.08	0.00	5.3	0.016	0.019
			Central			
AB1	18	1.16	2.00	15.8	0.062	0.058
AB2	17	1.16	2.00	15.8	0.104	0.075
AB3	17	1.21	2.33	15.8	0.085	0.073
AB4	15	1.21	2.00	21.1	0.096	0.102
AB5	14	1.42	2.33	26.3	0.105	0.093
SK1	19	1.21	2.33	15.8	0.078	0.064
SK2	24	1.32	2.00	26.3	0.060	0.062
Mean		1.35	2.07	19.6	0.084	0.075
(SE)		0.05	0.04	1.9	0.007	0.006
			South			
MT1	32	1.47	2.29	26.3	0.090	0.084
MT2	32	1.37	2.17	31.6	0.083	0.103
MT3	26	1.26	2.25	15.8	0.062	0.070
MT4	26	1.53	2.43	26.3	0.088	0.082
Mean		1.41	2.29	25	0.081	0.085
(SE)		0.08	0.11	3.3	0.006	0.007

		subsp. *megacephala*				
population	21.0	*1.45	2.21	*31.6	*0.126	*0.129
(SE)	2.2	0.03	0.06	2.7	0.008	0.009
subspecies	127	1.74	2.75	42.1	0.134	-
(SE)	-	0.05	0.25	-	0.035	-
		subsp. *lanulosa*				
population	21.5	*1.31	2.16	*23.1	*0.085	*0.084
(SE)	1.7	0.03	0.05	1.9	0.005	0.006
subspecies	310	2.05	3.22	47.4	0.115	-
(SE)	-	0.31	0.36	-	0.035	-

[1] Variables are as follows: N, sample size; A, mean number of alleles per locus; A_P, mean number of alleles per polymorphic locus; P, percent of loci that are polymorphic (95% criterion); H_E, expected heterozygosity; H_O, observed heterozygosity. * indicates values differ between taxa for population genetic statistics ($P < 0.05$).

Total genetic diversity at polymorphic loci (H_T) in *Achillea millefolium* subsp. *megacephala* was 0.296, compared to 0.254 in *A. millefolium* subsp. *lanulosa* (TABLE 5.4). Within population genetic diversity (H_S) was higher in *A. millefolium* subsp. *megacephala* (0.272) than in *A. millefolium* subsp. *lanulosa* (0.178). The among population differentiation (G_{ST}) was lower in the endemic (0.078) than the widespread taxon (0.300) (TABLE 5.4). G_{ST} values for geographic subdivisions of *A. millefolium* subsp. *lanulosa* were lower - north (0.011), central (0.222), and south (0.056). Wright's estimate for gene flow (Nm_W) for *A. millefolium* subsp. *megacephala* was 2.94 migrants per generation and for *A. millefolium* subsp. *lanulosa* it was 0.583 migrants per generation (TABLE 5.4). Nm_W values for geographic regions of *A. millefolium* subsp. *lanulosa* were 23.56 (north), 0.87 (central), and 4.22 (south).

TABLE 5.4. Genetic diversity statistics (Nei, 1973), and estimates of gene flow for populations of *Achillea millefolium* subsp. *lanulosa* from different geographic regions and the endemic subsp. *megacephala*. [1]

Taxon and location	H_T	H_S	D_{ST}	G_{ST}	Nm_W
subsp. *megacephala*	0.296	0.272	0.023	0.078	2.94
subsp. *lanulosa* [all]	0.254	0.178	0.076	0.300	0.58
North	0.245	0.242	0.003	0.011	23.56
Central	0.204	0.159	0.045	0.222	0.87
South	0.189	0.179	0.011	0.056	4.22

[1] Variables are as follows: H_T, total genetic diversity; H_S, genetic diversity within populations; D_{ST}, genetic diversity among populations; G_{ST}, proportion of genetic diversity among populations; Nm_W, number of migrants per generation.

Genetic identity values (I) for all pairs of populations were high . Intraspecific I values for populations of *Achillea millefolium* subsp. *megacephala* ranged from 0.968 to

0.999 with a mean of 0.988; for *A. millefolium* subsp. *lanulosa*, *I* values ranged from 0.919 to 1.000 with a mean of 0.961 (TABLE 5.5). The mean interspecific *I* value between *A. millefolium* subsp. *lanulosa* and *A. millefolium* subsp. *megacephala* was 0.943, with values ranging from 0.874 to 0.993. The endemic taxon had higher interspecific *I* values with central and north populations of the widespread taxon.

TABLE 5.5. Mean genetic identities (Nei, 1978) and ranges (in parentheses) for populations of *Achillea millefolium* subsp. *lanulosa* from different geographic regions and the endemic subsp. *megacephala*.

Location	Dunes	Central	South	North
Dunes	0.988			
	(0.968 - 0.999)			
Central	0.954	0.977		
	(0.881 - 0.993)	(0.934 - 1.000)		
South	0.922	0.943	0.995	
	(0.874 - 0.947)	(0.926 - 0.961)	(0.992 - 0.998)	
North	0.947	0.973	0.932	0.999
	(0.926 - 0.965)	(0.919 - 0.986)	(0.926 - 0.936)	(0.999 - 0.999)

The PCA is presented with OTUs (populations) plotted onto the derived variables (principal axes) and alleles plotted at the end of vectors of the individual alleles relative to the PCA axes (FIGURE 5.2). The PCA indicates the close association of populations from the sand dunes, and their more distant genetic relationship to populations of *Achillea millefolium* subsp. *lanulosa* (FIGURE 5.2). Populations from the central and north regions of *A. millefolium* subsp. *lanulosa* cluster together except for AB4 (Red Deer River, Alberta), which is between the groups formed by the north-central populations and the south populations (FIGURE 5.2). The loci important in differentiating populations of the two taxa are *Lap-2*, *Idh-1*, *Pgm-2*, and *Got-1*. Loci important in differentiating regional groups of *A. millefolium* subsp. *lanulosa* are *Pgi-2*, *Idh-2*, and *Mdh-3* (FIGURE 5.2).

DISCUSSION

Amount and pattern of genetic variation. The endemic *Achillea millefolium* subsp. *megacephala* has more genetic variability at the population level than its widespread relative *A. millefolium* subsp. *lanulosa*. Estimates of the mean number of alleles per locus, percent polymorphic loci, and heterozygosity were all higher in the endemic. Species with restricted geographic distributions typically have fewer polymorphic loci, fewer alleles per locus, and reduced heterozygosity (Gottlieb, 1973; Karron, 1987; Loveless and Hamrick, 1988; Hamrick and Godt, 1989; Pleasants and

Wendel, 1989; Hamrick et al., 1991; Bayer 1992; Sherman-Broyles et al. 1992; Baskauf, McCauley, and Eickmeier, 1994) though there are exceptions (Mashburn, Sharitz, and Smith, 1978; Bayer and Crawford, 1986; Karron et al., 1988; Linhart and Premoli, 1993). Mean values compiled by Hamrick and Godt (1989) for A (1.39), P (26.3), and H_E (0.063) in endemic taxa were all lower than the values found in *A. millefolium* subsp. *megacephala*. However, at the species level, mean values compiled by Hamrick and Godt (1989) for A (1.80), P (40.0), and H_E (0.096) in endemic taxa were comparable to the values found in *A. millefolium* subsp. *megacephala*.

Karron (1987, 1991) has suggested caution when drawing conclusions about associations when comparing population genetic information from unrelated taxa and has suggested that closely related widespread congeners be used for comparison with rare species, as they often share ecological and historical traits. We considered the closely related widespread *Achillea millefolium* subsp. *lanulosa* as the control to examine aspects of genetic variation for the endemic *A. millefolium* subsp. *megacephala* just as the widespread progenitor species have served as the control in other studies of genetic

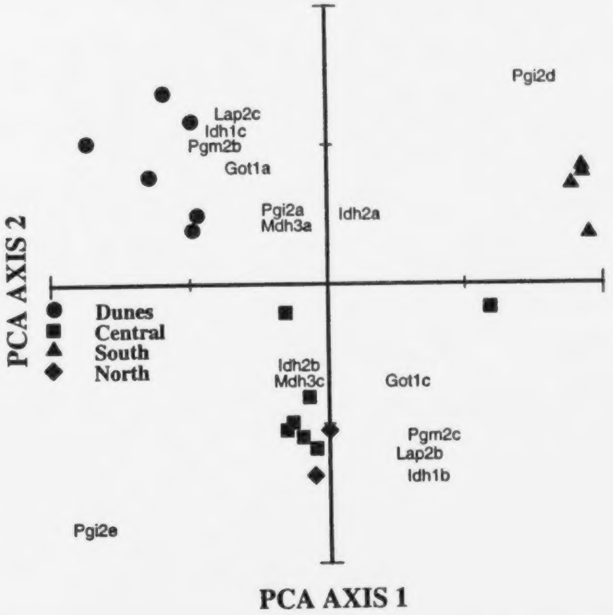

FIGURE 5.2. Principal components analysis of allele frequencies from populations of *Achillea millefolium* subsp. *lanulosa* and *A. millefolium* subsp. *megacephala*. The first two principal components explain 42.8% and 26.2% of the total variance, respectively. Positions for OTUs (populations) and variables (alleles) are presented.

diversity in Athabasca sand dune endemic species (Purdy, Bayer, and Macdonald, 1994 [chapter 2]; Purdy and Bayer, 1995a [chapter 3], 1995b [chapter 4]). Previous studies on the Athabasca sand dune endemics *Stellaria arenicola* (Purdy, Bayer, and Macdonald, 1994 [chapter 2]), *Deschampsia mackenzieana* (Purdy and Bayer, 1995a [chapter 3]), and *Salix silicicola* (Purdy and Bayer, 1995b [chapter 4]) revealed the endemic species to be genetically depauperate relative to closely related widespread taxa. Why then, would the relationship between *A. millefolium* subsp. *megacephala* and its widespread relative be different?

There is considerable evidence that suggests bottlenecks and founder effects play a significant role in governing patterns of genetic variability in colonizing species (see Barrett and Kohn, 1991 for review). Theoretical and empirical evidence suggest that genetic bottlenecks have a large effect on allelic diversity and also affect heterozygosity (Wright, 1931; Nei, Maruyama, and Chakraborty, 1975; Leberg, 1992). Therefore, levels of genetic variation within populations of *Achillea millefolium* would be dependent on the amount of genetic variation in the founding individuals, the length of time the population remained small, and levels of gene flow.

Once populations are established, individuals of *Achillea millefolium* can survive and spread by vegetative means as well as by sexually produced seeds which are the product of insect-pollinated outcrossing events as individuals are self-incompatible (Warwick and Black, 1982). Mean values compiled by Hamrick and Godt (1989) for A (1.47), P (29.4), and H_E (0.103) in taxa with sexual and asexual reproduction were comparable to the values found in *A. millefolium* subsp. *lanulosa*. On the Athabasca sand dunes, however, the opportunity for continued asexual reproduction in a population is minimal. The nature of the rolling dunes found in the Thomson Bay and William River dune fields where many of the endemic species are common ensures recruitment of new individuals occurs by sexual means alone (Hermesh, 1972; Raup and Argus, 1982). Seedlings are common in dune slacks where the water table is at or near the surface (Raup and Argus, 1982). As the rolling dunes shift, the plants established in the dune slacks become buried by sand, from anywhere between 0.5 to 12 metres (Hermesh, 1972). This burial is one of the most important selection forces determining the persistence of species on the Athabaca sand dunes (Raup and Argus, 1982). However, few plants survive the subsequent ablation of sand as the dune moves on (B. Purdy, personal observation). The only possibility for persistence in this habitat is for new individuals to establish from seed in the newly forming dune slacks. Thus, populations of the endemic *A. millefolium* subsp. *megacephala* may rely more on sexual reproduction to maintain populations than *A. millefolium* populations found in other habitats. This may help explain the greater genetic variation at the population level found in this endemic.

Achillea millefolium subsp. *megacephala* populations were found to have slightly higher total genetic diversity (H_T), and higher within-population genetic diversity (H_S), than the widespread *A. millefolium* subsp. *lanulosa*, different from the pattern found in other studies (Hamrick and Godt, 1989). The value of H_T found for the sand dune endemic was comparable to the mean of values reported by Hamrick and Godt (1989) whereas the value of H_S is considerably higher. Total and within-population genetic diversity in *A. millefolium* subsp. *lanulosa* was considerably less than that reported for other widespread taxa or for species with sexual and asexual means of reproduction. Some other population genetic studies have found the widespread species to be no more genetically diverse than the endemic (Bayer and Crawford, 1986; Karron et al., 1988; Linhart and Premoli, 1993), though these studies are notable exceptions.

Levels of among-population differentiation (G_{ST}) were considerably lower in *Achillea millefolium* subsp. *megacephala* than in *A. millefolium* subsp. *lanulosa*, though populations of the widespread taxon were collected over a greater geographic area. Geographic subdivisions of *A. millefolium* subsp. *lanulosa* have lower G_{ST} values, indicating that populations within a region are more similar to one another than populations among regions. Gene flow estimates for the north and south geographic subdivisions of *A. millefolium* subsp. *lanulosa* and for *A. millefolium* subsp. *megacephala* were moderate to high for insect-pollinated herbaceous perennials (Hamrick, 1987).

Though *Achillea millefolium* subsp. *megacephala* has higher population genetic variation than *A. millefolium* subsp. *lanulosa*, it has lower total allelic diversity, having 23 alleles at polymorphic loci compared to 30 alleles in the progenitor. However, where polymorphisms do exist at a locus in *A. millefolium* subsp. *megacephala*, the allele frequencies were more evenly distributed than in *A. millefolium* subsp. *lanulosa*. Higher levels of sexual reproduction in plant populations on the Athabasca sand dunes may contribute to the broader distribution of allele frequencies found in *A. millefolium* subsp. *megacephala*.

***Origin of Achillea millefolium* subsp. *megacephala*.** Recently derived species have been predicted to exhibit: 1) less genetic variation than the progenitor; 2) a subset of the allelic diversity found in the progenitor with few, if any, unique alleles; and 3) high genetic similarity with the progenitor taxon (Gottlieb, 1973; Pleasants and Wendel, 1989). These predictions have been supported by a number of studies (Gottlieb, 1973, 1974; Crawford and Smith, 1982a, 1982b; Crawford, Ornduff, and Vasey, 1985; Gottlieb, Warwick, and Ford, 1985; Loveless and Hamrick, 1988; Pleasants and Wendel, 1989). In studies of the genetic relationship between the derivative and progenitor species of other sand dune endemics (Purdy, Bayer, and Macdonald, 1994 [chapter 2]; Purdy and Bayer, 1995a [chapter 3], 1995b [chapter 4]) these predictions were supported.

However, in the present study the relationship between the derivative species and its widespread progenitor is not as clear. *Achillea millefolium* subsp. *megacephala* had higher population level genetic variation than its progenitor. In addition, the endemic had six unique alleles, though only three of these had a frequency greater than 0.05 in any one population. The derivative and progenitor taxa did however have a high genetic similarity. Interspecific *I* values between the two taxa were slightly lower than intraspecific *I* values found among the geographic subdivisions of *A. millefolium* subsp. *lanulosa*. Interspecific *I* values between progenitor-derivative species pairs reported for *Stellaria arenicola* (Purdy, Bayer, and Macdonald, 1994 [chapter 2]), *Deschampsia mackenzieana* (Purdy and Bayer, 1995a [chapter 3]) and *Salix silicicola* (Purdy and Bayer, 1995b [chapter 4]) from the Athabasca sand dunes are comparable to the values reported here. The high genetic identities support previous suggestions of a recent Holocene origin for the sand dune endemics (Argus and Steele, 1979; Raup and Argus, 1982; Macdonald et al., 1987).

Conclusion. *Achillea millefolium* subsp. *megacephala* differs from other Athabasca sand dune endemics studied previously in that its populations maintain greater genetic variation than the related widespread taxa. It may be that the reliance on sexual reproduction for persistence on the sand dunes results in the maintenance of higher levels of genetic diversity in this habitat, although we can only speculate as to the reasons for this pattern. The widespread and ecologically diverse *A. millefolium* subsp. *lanulosa* has lower levels of genetic variation than most widespread species, though there are other examples in the literature of this pattern in species with similar geographic distributions and high ecological amplitude, notably species of *Typha* (Mashburn, Sharitz, and Smith, 1978) having no detectable electrophoretic variation.

Populations of *Achillea millefolium* subsp. *megacephala* are restricted to the Thomson Bay and William River dune fields on the south shore of Lake Athabasca. The subspecies is listed using nature conservancy rankings as nationally and provincially extremely rare (Argus and Pryer, 1990), and is a candidate for the endangered species list in Canada, though no status report has been completed to date. The species co-occurs with critical populations of other Athabasca sand dune endemics (B. Purdy, personal observation). Because the entire sand dune region in Saskatchewan has been designated a wilderness provincial park, the most restrictive park status in the province, development pressures are non-existant. Demographic monitoring of *A. millefolium* subsp. *megacephala* and other endemics on the large dune fields will be important to ensure the persistence of these species, and to increase our understanding of the life history dynamics of endemic species on the Athabasca sand dunes.

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Chapter Six

Allozyme variation in populations of the Athabasca sand dune endemic *Armeria maritima* subsp. *interior* (Plumbaginaceae) and its widespread progenitor *A. maritima* subsp. *labradorica* from the high arctic in Canada

ABSTRACT. Endemic species are hypothesized to have little genetic variation because of genetic drift, bottlenecks, inbreeding, or other factors. This study investigated genetic variation in the Athabasca sand dune endemic, *Armeria maritima* subsp. *interior*, a threatened species in Canada, and the closely related widespread taxon, *Armeria maritima* subsp. *labradorica*. We examined electrophoretic patterns at 27 loci in six populations of the endemic and three populations of the putative progenitor. *Armeria maritima* subsp. *interior* was polymorphic at only one isozyme locus in one population whereas up to three loci were polymorphic in populations of *Armeria maritima* subsp. *labradorica*. Both taxa had considerably less genetic variation than is usually found in species with similar life history traits and geographic distributions. The lack of genetic variation in the endemic taxon is probably due to a genetic bottleneck after the species became established on the Athabasca sand dunes as populations from all dune fields shared the same alleles at all loci, except the one population observed to have two alleles at *Pgi-2*.

INTRODUCTION

Knowledge of the amount and distribution of genetic diversity in endemic plant species may contribute to our understanding of the evolutionary history of the species (Loveless and Hamrick, 1988). Evidence suggests populations of species with restricted distributions generally contain less genetic variation than do populations of related widespread taxa (Karron, 1987; Hamrick and Godt, 1989). Genetic drift, founder effects, and/or strong directional selection may be responsible for observed low levels of genetic variation in endemic taxa (Karron, 1987). Population genetic information may also be used to suggest appropriate management strategies for endemic species if they are endangered (Falk and Holsinger, 1991), as it is generally agreed that genetic diversity is necessary to preserve the long-term evolutionary potential of a species (Holsinger and Gottlieb, 1991).

Armeria maritima subsp. interior

Although the boreal forest contains few endemic taxa (Kruckeberg and Rabinowitz, 1985), on the south shore of Lake Athabasca in northern Saskatchewan, Canada, a number of endemic plant species can be found (Abouguendia et al., 1981; Raup and Argus, 1982). These taxa are restricted to the Athabasca sand dunes and occur primarily in areas of actively blowing sand (Raup and Argus, 1982; Rowe and Abouguendia, 1982). Rare features of the Athabasca sand dunes are the stable gravel pavements that have polished ventifacts, evidence that suggests the pavements are of considerable age (Raup and Argus, 1982).

The tap-rooted perennials *Armeria maritima* (Mill.) Willd. subsp. *interior* (Raup) Porsild and *Silene acaulis* L. f. *athabascensis* Argus are the only endemics to occur primarily on the gravel pavements (Raup and Argus, 1982). *Armeria maritima* subsp. *interior* is thought to be derived from *A. maritima* subsp. *labradorica* (Wahl.) Hult. which occurs far north of the sand dunes along the arctic coast and in a few inland locations near Great Slave Lake and the Mackenzie and Thelon River systems (Porsild, 1955; Argus, 1981). The endemic differs from other North American *Armeria* by its totally glabrous calyx tube (Raup, 1936; Porsild, 1955).

This study was initiated to compare levels of genetic variation within and among populations of the endemic *Armeria maritima* subsp. *interior* from the Athabasca sand dunes and the widespread *A. maritima* subsp. *labradorica* from the high arctic. We were interested in comparing the population genetics of *A. maritima* subsp. *interior* with other Athabasca sand dune endemics (Purdy, Bayer, and Macdonald, 1994 [chapter 2]; Purdy and Bayer, 1995a [chapter 3], 1995b [chapter 4], unpublished [chapter 5]) and populations of *A. maritima* studied from elsewhere in the world (Vekemans, Lambert, and Lefèbvre, 1992). We also wanted to establish population genetic information for *A. maritima* subsp. *interior*, a threatened species in Canada.

MATERIALS AND METHODS

Mature inflorescences were collected from plants in each of six populations of the endemic *Armeria maritima* subsp. *interior* and three populations of the related widespread *A. maritima* subsp. *labradorica* (TABLE 6.1 and FIGURE 6.1). Seeds were collected instead of established plants in order to minimize impacts on small populations of the because live plant collection in the arctic was difficult. Seeds were germinated and seedlings were subsequently established and maintained in Terra-Lite 2000 soil (Grace Horticultural Products, Ajax, Ontario) in Spencer-Lemaire containers at the University of Alberta phytotron.

Enzyme electrophoresis generally followed Purdy, Bayer, and Macdonald (1994 [chapter 2]). Young leaves were removed from each plant and ground immediately in Tris-HCl grinding buffer (Purdy, Bayer, and Macdonald, 1994 [chapter 2]). The supernatant was absorbed onto filter paper wicks, frozen at -20^{0} C overnight, and electrophoresed the following morning. The filter paper wicks were loaded onto 12% starch gels.

In this study, fourteen enzyme systems were resolved on buffer systems I, II, and III of Purdy, Bayer, and Macdonald (1994 [chapter 2]). Alcohol dehydrogenase (ADH), glutamate dehydrogenase (GDH), glutamate oxalate-transaminase (GOT), leucine aminopeptidase (LAP), phosphoglucose isomerase (PGI), and triose-phosphate isomerase (TPI) were resolved on system I. Aldolase (ALD), isocitrate dehydrogenase (IDH), malate dehydrogenase (NADP[ME]), and shikimic acid dehydrogenase (SKD) were resolved on system II. Glyceraldehyde-3-phosphate dehydrogenase (G3PDH), malate dehydrogenase (NAD[MDH]), 6-phosphogluconate dehydrogenase (PGD), and phosphoglucose mutase (PGM) were resolved on system III. Electrophoretic conditions were the same as Purdy, Bayer, and Macdonald (1994 [chapter 2]).

TABLE 6.1. Population designation, collection location and habitat for six populations of *Armeria maritima* subsp. *interior* and three populations of subsp. *labradorica* sampled in this study.

Pop.	Population location and habitat.
	A. maritima subsp. *interior*
INT1	South Thomson dune field. Lat. 59^{0} 00' N., Long. 109^{0} 08' W., elev. 270 m. Active sand dunes.
INT2	William River dune field. Lat. 59^{0} 03' N., Long. 109^{0} 15' W., elev. 244 m. Gravel pavement.
INT3	Cantara Lake dune field. Lat. 59^{0} 06' N., Long. 108^{0} 49' W., elev. 230 m. Gravel pavement.
INT4	Central Thomson dune field. Lat. 59^{0} 03' N., Long. 109^{0} 05' W., elev. 270 m. Active sand dunes.
INT5	Central Yakow Lake dune field. Lat. 59^{0} 10' N., Long. 108^{0} 00' W., elev. 240. Active sand dunes.
INT6	Eastern Yakow Lake dune field. Lat. 59^{0} 10' N., Long. 107^{0} 55' W, elev. 255 m. Gravel pavement.
	A. maritima subsp. *labradorica*
LAB1	Victoria Island, N.W.T. Gravel beach habitat along the Arctic Ocean.
LAB2	Fosheim Peninsula, Ellesmere Island, N.W.T. Gravel beach habitat along the Arctic Ocean.
LAB3	Eureka Sound, Ellesmere Island, N.W.T. Gravel beach habitat along the Arctic Ocean.

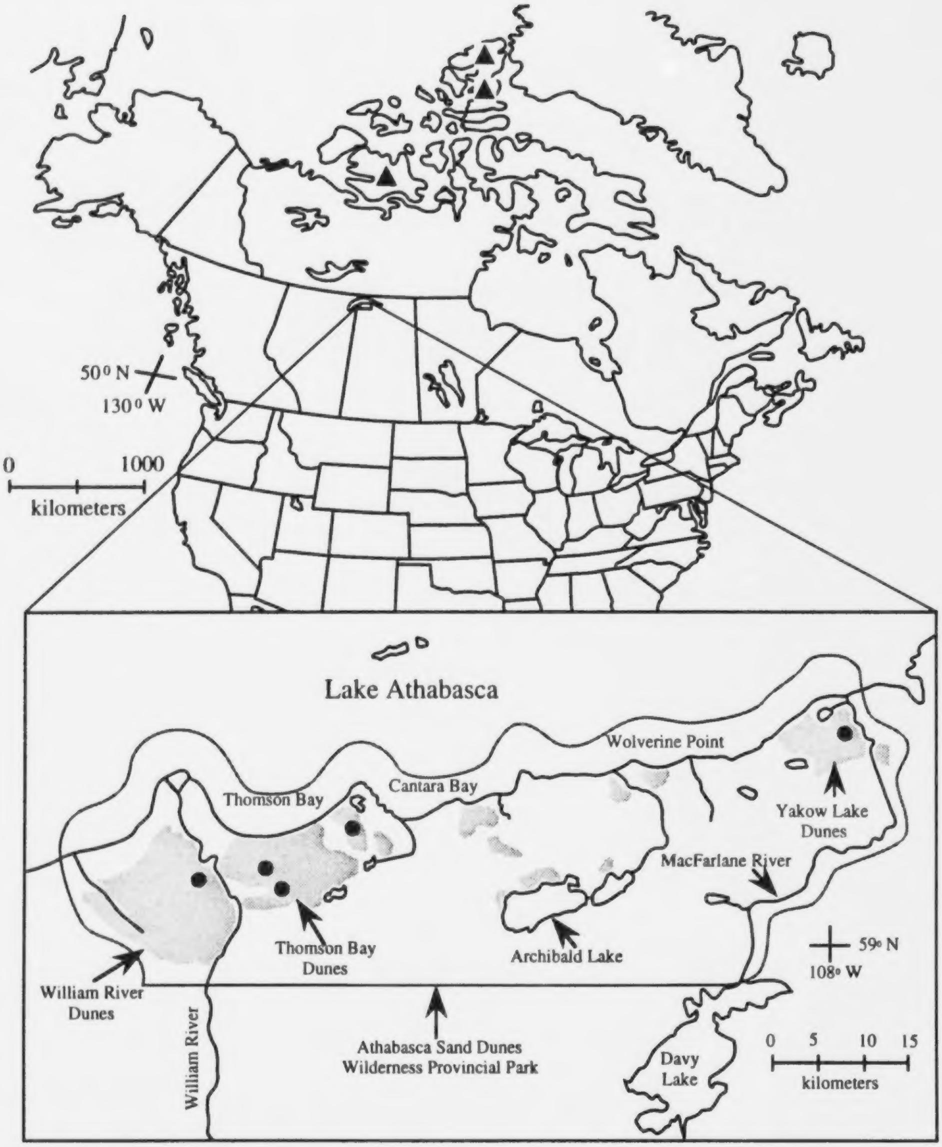

FIGURE 6.1. Location of populations of the geographically widespread *Armeria maritima* subsp. *labradorica* (triangles) from the high arctic and the endemic *A. maritima* subsp. *interior* (circles) from the Athabasca sand dunes sampled in this study.

Enzymatic assays followed Soltis et al. (1983) except for ADH (Wendel and Weeden, 1989). Isozymes were numbered sequentially with the most anodal isozyme designated 1 (e.g., MDH-1), encoded by locus 1 (e.g., *Mdh-1*). Similarly, allozymes were denoted alphabetically with the most anodal as A (encoded by allele *a*). Bands were categorized as isozymes and allozymes by observing segregation patterns among individuals in the populations sampled in light of the typical subunit structure and subcellular compartmentalization (Gottlieb, 1981; Weeden and Wendel, 1989). For each population, the mean number of alleles per locus (A), the percentage of polymorphic loci (P), expected heterozygosity (H_E), and observed heterozygosity (H_O) were calculated. We also calculated genetic identities (Nei, 1978). All calculations were made using BIOSYS (Swofford and Selander, 1989).

TABLE 6.2. Allele frequency data for polymorphic loci from six populations of *Armeria maritima* subsp. *interior* and three populations of *A. maritima* subsp. *labradorica*.

Locus /	subsp. *interior*						subsp. *labradorica*		
allele	INT1	INT2	INT3	INT4	INT5	INT6	LAB1	LAB2	LAB3
Mdh-1									
a	-	-	-	-	-	-	0.045	-	-
b	1.000	1.000	1.000	1.000	1.000	1.000	0.955	1.000	1.000
Mdh-4									
a	-	-	-	-	-	-	0.375	0.400	0.095
b	1.000	1.000	1.000	1.000	1.000	1.000	0.625	0.600	0.905
Pgi-2									
a	-	-	-	0.043	-	-	0.146	0.100	0.083
b	1.000	1.000	1.000	0.957	1.000	1.000	0.854	0.900	0.917

RESULTS

The 14 enzyme systems assayed in this study are coded by 27 putative loci. Twenty-four of the loci were monomorphic in all populations: *Adh-1, Ald-1, Ald-2, G3pdh-1, G3pdh-2, Gdh-1, Got-1, Idh-1, Idh-2, Lap-1, Lap-2, Mdh-2, Mdh-3, Me-1, Me-2, Pgd-1, Pgd-2, Pgm-1, Pgm-2, Pgi-1, Skd-1, Skd-2, Tpi-1*, and *Tpi-2*. Three loci were polymorphic in at least one population: *Mdh-1, Mdh-4,* and *Pgi-2* (TABLE 6.2). Only one population (INT4) and one locus (*Pgi-2*) were polymorphic in *Armeria maritima* subsp. *interior* whereas three loci were polymorphic in *A. maritima* subsp. *labradorica* (TABLE 6.2). Both taxa shared the same most common allele at all loci (TABLE 6.2).

TABLE 6.3. Summary of allozyme variation in *Armeria maritima* subsp. *interior* and *A. maritima* subsp. *labradorica*. [1]

Taxon	No. of Pops.	N	A	P	H_E	H_O
subsp. *interior*	6	22.6	1.01	0.6	0.001	0.001
(SE)		0.2	0.01	0.1	0.001	0.001
subsp. *labradorica*	3	21.9	1.09	8.6	0.022	0.021
(SE)		0.1	0.03	1.2	0.009	0.008

[1] N = mean sample size per population, A = mean number of alleles per locus, P = % polymorphic loci, H_E = expected heterozygosity, H_O = observed heterozygosity.

Although a polymorphism was observed at one locus in *Armeria maritima* subsp. *interior*, the genetic diversity detected in this taxon was essentially zero: $A = 1.01$, $P = 0.6$, $H_E = 0.001$, $H_O = 0.001$ (TABLE 6.3). Values for A (1.09), P (8.6), H_E (0.022), and H_O (0.021) were higher in *A. maritima* subsp. *labradorica* (TABLE 6.3). Intraspecific genetic identities (I) were 1.000 between all populations of the endemic taxon and ranged from 0.997 to 1.000 (mean = 0.998) between populations of the widespread taxon (TABLE 6.4). Interspecific I values ranged from 0.994 to 1.000 with a mean of 0.996 (TABLE 6.4).

TABLE 6.4. Mean genetic identities (Nei, 1978) and ranges (in parentheses) for populations of *Armeria maritima* subsp. *interior* and *A. maritima* subsp. *labradorica*.

Taxon	subsp. *interior*	subsp. *labradorica*
subsp. *interior*	1.000 (1.000 - 1.000)	
subsp. *labradorica*	0.996 (0.994 - 1.000)	0.998 (0.997 - 1.000)

DISCUSSION

The populations of *Armeria maritima* subsp. *interior* we sampled had almost no detectable isozyme variation as only one locus (*Pgi-2*) in one population (INT4) was found to be polymorphic. Although species with restricted ranges typically have less genetic variation than related widespread taxa (Karron, 1987; Hamrick and Godt, 1989; Pleasants and Wendel, 1989; Bayer, 1992; Sherman-Broyles et al., 1992; Baskauf, McCauley, and Eickmeier, 1994), only a few isozyme studies of endemic taxa have found less genetic variation than that reported here (Ledig and Conkle, 1983; Schwartz, 1985; Waller, O'Malley, and Gawler, 1987; Lesica et al., 1988; Soltis, Soltis, and Lang, 1991). Values for A (1.01), P (0.6), and H_E (0.001) were all significantly lower in *A. maritima* subsp. *interior* than the mean of values compiled by Hamrick and Godt (1989) for endemic taxa ($A = 1.39$; $P = 26.3$; and $H_E = 0.063$).

Populations of the widespread *Armeria maritima* subsp. *labradorica* sampled in this study from the high arctic also had very low amounts of genetic variation (A =1.09; P = 8.6; and H_E = 0.022), certainly less than that expected for either a widespread or an endemic species (Hamrick and Godt, 1989). The populations we sampled of this widespread taxon approach the northern limits of the range for the species (Porsild, 1955; Porsild and Cody, 1980), especially LAB2 and LAB3 from Ellesmere Island. The more central population from Victoria Island (LAB1) was polymorphic at three loci compared to two loci for the Ellesmere populations.

The possible lack of diversity in geographically marginal populations has been the subject of several investigations. Tremblay and Simon (1989) and Perry and Knowles (1989) found relatively high amounts of genetic variability in marginal populations of *Picea glauca* (Moench)Voss and geographically isolated populations of *Acer saccharum* Marsh, respectively. In contrast, a number of studies have found marginal populations to have considerably less genetic variation than central populations. Marginal populations of *Sarracenia purpurea* L. (Schwaegerle and Schaal, 1979), *Pinus contorta* Dougl. (Yeh and Layton, 1979), *Pinus jeffreyi* Grev. and Balf. (Furnier and Adams, 1986), *Campanula punctata* (Inoue and Kawahara, 1990), *Antennaria rosea* (Bayer, 1991), and *Lilium parryi* Wats.(Linhart and Premoli, 1994) had less genetic variability than geographically central ones. Founder events and bottlenecks play a significant role in governing patterns of genetic diversity in colonizing populations (Barrett and Kohn, 1991), and would affect amounts of variation in populations at the margins of a species' range.

Armeria maritima is a morphologically and ecologically polymorphic species, and is geographically widespread throughout much of the northern hemisphere (Woodell and Dale, 1993). In most of Europe *A. maritima* has a heteromorphic breeding system and is self-incompatible (Vekemans et al., 1990). In the circumpolar arctic tundra, populations are monomorphic and self-compatible (Baker, 1966). The only previous isozyme study on this species investigated genetic diversity and relationships among predominantly heteromorphic populations from maritime and heavy-metal contaminated sites in western Europe (Vekemans, Lambert, and Lefèbvre, 1992). Though metal-tolerant populations had lower genetic variation than maritime populations (A =2.26 vs. 2.73, H_E = 0.352 vs.

0.494), all sites were found to have considerably higher genetic variation than the *A. maritima* populations we sampled from North America. There are no previous isozyme studies from populations of *A. maritima* that are self-compatible. The low levels of isozyme diversity observed in *A. maritima* populations sampled in this study may be due to a number of factors: the Eurasian origin of self-compatible populations (Vekemans et al., 1990), high levels of selfing (all individuals set seed in the absence of pollinators in the greenhouse), and the fact that all the populations sampled in this study were geographically marginal.

The Athabasca sand dune endemics *Stellaria arenicola* Raup (Purdy, Bayer, and Macdonald, 1994 [chapter 2]), *Deschampsia mackenzieana* Raup (Purdy and Bayer, 1995a [chapter 3]), and *Salix silicicola* Raup (Purdy and Bayer, 1995b [chapter4]) were all found to have less genetic variation than closely related widespread species from which they were thought to have evolved. However, these endemic taxa still had considerable genetic diversity relative to that found in either the rare endemic *Armeria maritima* subsp. *interior* or the widespread *A. maritima* subsp. *labradorica*.

Progenitor populations of endemic taxa including *Armeria maritima* existed south of the ice-sheets during the Pleistocene and migrated north as the ice retreated (Argus and Steele, 1979). Colonization of the sand dune environment would have presumably involved considerable directional selection for traits that enabled survival in a unique environment within the boreal forest. *Armeria maritima* subsp. *interior* does not survive in the same habitat occupied by the other sand dune endemics, but instead occurs primarily on the stable gravel pavements where few other plant species survive (Raup and Argus, 1982). A genetic bottleneck on the Athabasca sand dunes may have resulted in the fixation of a quantitative character considered extremely rare in *Armeria maritima*, a totally glabrous calyx tube (Porsild, 1955). During this genetic bottleneck, much of the isozyme variation would have been lost as well. Further investigation of genetic diversity in populations of *A. maritima* subsp. *labradorica* from the Keewatin district of the N.W.T. where progenitor populations are thought to occur (Argus and Steele, 1979), and the arctic coast will be necessary to quantify the nature of the genetic bottleneck that may have occurred in populations of *A. maritima* subsp. *interior*.

What are the implications of these data for management of *Armeria maritima* subsp. *interior*, a threatened species in Canada? Populations of this endemic are restricted to the William River, Thomson Bay, and Yakow Lake dune fields where they occur on gravel pavements and wet dune slacks between small rolling dunes. The stable populations (e.g., older) with individuals having large basal rosettes occur primarily on gravel pavements. Several large populations were also found at the south end of the Thomson Bay dune field between shallow rolling dunes. This area includes INT4, the only population found to have any isozyme variation. Whereas populations on the gravel pavements appear relatively stable, comprised of predominantly old (large rosettes) and some young (small rosettes) individuals, the rolling dunes provide excellent habitat in the wet dune slacks for seedling establishment, which appears to result in considerable recruitment of seedlings (B. Purdy, personal observation). In this habitat, however, individuals are eventually buried by sand. While our observations suggest that the populations near the south end of Thomson Bay dune field are the largest, at present (and have the only isozyme diversity we observed), should the climate become drier, these areas would experience increased aeolian activity (Abouguendia et al., 1981; Raup and Argus, 1982) and become inhospitable for *A. maritima* subsp. *interior*. Thus, gravel pavement populations of *A. maritima* subsp. *interior* might be most important for conservation during dry climatic periods.

The impact of environmental, demographic, and genetic stochasticity is reduced when large numbers of individuals and populations are preserved. For this reason, all populations of *Armeria maritima* subsp. *interior* should be preserved until more detailed studies on genetic variation and population biology are conducted. The genetic variation within and among populations of this rare sand dune endemic and its progenitor is currently being assessed with RAPD's [see Williams et al., (1990) for an introduction to this procedure], a technique we hope will reveal more information on the genetic structure of populations in these species.

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Chapter Seven
General Conclusion

Origin and Evolution of the Endemic Plants on the Athabasca Sand Dunes. In this study, we compared the population genetics of five Athabasca sand dune endemic plant taxa with their related widespread species from which they were thought to have evolved. No previous studies have investigated amounts and patterns of genetic variation within a group of unrelated endemic taxa that have evolved in and share the same habitat, such as the endemic plants of the Athabasca sand dunes. While the results largely conformed with the theoretical and empirical evidence that suggests restricted species have less genetic variation than widespread species, each study revealed different insights into the evolution of that particular endemic plant.

The Athabasca sand dunes in northwestern Saskatchewan are believed to have formed about 8,500 B.P., as the waters of glacial Lake McConnell, the precursor to Lake Athabasca, receded, exposing sandy glaciofluvial and lacustrine sediments eroded from the Precambrian Athabasca sandstone (Raup and Argus, 1982). The geographically closest record of Holocene vegetation changes in the Lake Athabasca region suggests plant communities comprising a mixture of tundra and grassland elements (Ritchie, 1987) established in the vicinity about 8,600 years ago (Vance, 1985). Thus, plant species would have been available to colonize the Athabasca sand dunes as soon as they formed.

The evolution of taxa in the Holocene has occurred in many sand dune systems, which are said to be the equivalent of habitat islands (Bowers, 1984; Pavlick, 1989). Today, the Athabasca sand dunes are a habitat island in the boreal forest. What is unique is that, despite the occurrence of few endemic taxa in boreal and arctic regions (Kruckeberg and Rabinowitz, 1985), the Athabasca sand dunes harbor ten endemic plant taxa, comparable to the high levels of endemism found in other sand dune systems in southern regions of North America (Bowers, 1984; Pavlick, 1989).

Stellaria arenicola (Purdy, Bayer, and Macdonald, 1994 [chapter 2]) and *Deschampsia mackenzieana* (Purdy and Bayer, 1995 [chapter 3]) have both evolved while sympatric with populations of their progenitor species on the Athabasca sand dunes.

Despite the close association between the progenitor and endemic populations, these endemics were found to have less population genetic variation than the widespread species. The tetraploid nature of *D. mackenzieana* isolated it from the adjacent diploid gene pool of *D. cespitosa*. Evidence also suggested that a genetic bottleneck at the time of polyploidization was responsible for the lack of genetic diversity in this endemic. In contrast, the sympatric evolution of the endemic *S. arenicola* has probably resulted in higher population genetic variation than would occur had the endemic evolved allopatrically, because gene flow can still occur between the endemic and the progenitor *S. longipes*. A shift to higher levels of inbreeding in *S. arenicola* may have aided the rapid evolution of the endemic by allowing the fixation of adaptive gene complexes and by reducing gene flow with sympatric populations of the progenitor *S. longipes*.

In both species pairs, the progenitor populations from the Athabasca sand dunes were more related to the endemic species than to allopatric populations of the same species sampled from other habitats. In *Stellaria arenicola* only one unique allele was detected, whereas sand dune populations of the endemic and the progenitor *S. longipes* shared ten alleles not found in populations of *S. longipes* in other habitats (Purdy, Bayer, and Macdonald, 1994 [chapter 2]). *Deschampsia mackenzieana* had no unique alleles but shared one allele with sand dune populations of *D. cespitosa* that was not found in progenitor populations sampled from other regions of North America(Purdy and Bayer, 1995 [chapter 3]). This suggests the endemics have evolved from the sympatric gene pool of the progenitor species.

Salix silicicola (Purdy and Bayer, 1995b [chapter 4]) and *Armeria maritima* subsp. *interior* [chapter 6] are two endemics that have evolved from arctic ancestors and are presently allopatric with populations of the progenitor taxa. Both endemics had less genetic variation than the related widespread taxon. *Salix alaxensis*, the progenitor to *S. silicicola*, had an excess of heterozygotes, perhaps indicating heterozygosity confers a fitness advantage in this widespread taxon. In contrast, *S. silicicola* was found to have an overall deficiency of heterozygotes. Directional selection for sand dune adapted traits linked to isozyme loci or higher levels of biparental inbreeding may be responsible for the heterozygote deficiency in the endemic willow. Alternatively, especially if gene flow occurs over smaller distances in the sand dune willow populations, the heterozygote deficiency may be due to the Wahlund effect (Hartl, 1980).

Armeria maritima subsp. *interior* differs from the other endemics investigated here in that it lacks the traits considered to be adaptive to an active sand dune environment (e.g., rapid stem elongation, tomentose leaves). It occurs only rarely in areas where the sand is active and, in these instances, predominantly in dune slacks between smaller rolling dunes. We detected almost no genetic variation in this endemic, though populations of the progenitor, *A. maritima* subsp. *labradorica*, were also found to have little genetic variation [chapter 6]. *Armeria maritima* subsp. *interior* shows fixation for a totally glabrous calyx tube, a trait considered extremely rare among North American species of *A. maritima*. A genetic bottleneck may have resulted in the fixation of this quantitative character in early populations of *A. maritima* subsp. *interior*, and the loss of considerable genetic variation as well.

Few widespread species can be found in more habitats in temperate and subarctic regions than members of the *Achillea millefolium* complex. This species complex has evolved a variety of ecological races adapted to specific environmental conditions, enabling it to occupy a diversity of environments (Clausen, Keck, and Hiesey, 1948). *Achillea millefolium* subsp. *megacephala* is an endemic of the Athabasca sand dunes, and is related to the widespread *A. millefolium* subsp. *lanulosa*. Unlike the previously mentioned derivative-progenitor and endemic-widespread species pairs, *A. millefolium* subsp. *megacephala* was found to have more genetic variation within populations than *A. millefolium* subsp. *lanulosa* [chapter 5]. Populations of the progenitor taxon, though not found on the sand dunes themselves, have been collected in the vicinity of the Athabasca sand dunes, and could be considered parapatric with the endemic. We did note that, unlike habitats often colonized by *A. millefolium* where asexual reproduction is extensive, populations of *A. millefolium* subsp. *megacephala* on the Athabasca sand dunes must rely on sexual reproduction in order to survive. High levels of sexual reproduction may be partly responsible for the higher levels of genetic variation detected in this endemic relative to populations of its widespread progenitor.

All of the endemic species shared high genetic identities with progenitor populations, regardless of the sympatric or allopatric nature of their respective distributions. These data support previous suggestions (Argus and Steele, 1979; Raup and Argus, 1982; Macdonald et al., 1987) that the endemics have evolved on the Athabasca sand dunes during the Holocene. The lack of isozyme divergence seen in these endemics probably reflects their relatively recent origin.

Genetic Variation in Rare Plants. Stebbins (1942) was one of the first biologists to suggest that endemic taxa were genetically depauperate, though the techniques to readily test this hypothesis were not available at that time. Three decades later, Drury (1974) noted that, despite such a prediction by Stebbins (1942) and many others, few had measured genetic variation in rare and endemic taxa. However, throughout the 1970's and 1980's, the number of studies using starch gel electrophoresis to investigate levels of genetic diversity in plant species increased dramatically (*in* Brown, 1979; Gottlieb, 1977, 1981; Crawford, 1983; Loveless and Hamrick, 1984; Hamrick and Godt, 1989).

Surveys of allozyme variation in plants have supported theoretical predictions that species with limited ranges and small populations will exhibit low levels of genetic polymorphism (*in* Karron, 1987; Hamrick and Godt, 1989; Pleasants and Wendel, 1989; Soltis and Soltis, 1991). However, some studies have found severely restricted taxa to have almost as much genetic variation as widespread species (*in* Karron et al., 1988; Kuittinen et al., 1991; Linhart and Premoli, 1993). Part of the reason for these variable results among studies is because of the diversity of species, floristic ages, and enzyme systems investigated. Unrelated taxa have often been studied in different laboratories, which score different loci, and employ different isozyme techniques. Some loci have more alleles than others (Gottlieb, 1981), so comparisons involving different sets of genes in different taxa may be misleading (Simon and Archie, 1985). For this reason, Karron (1987, 1991) emphasized the importance of investigating genetic diversity among closely related restricted and widespread species as they often have similar phylogenetic histories, ecological features, and are studied in a single laboratory.

Only a few taxonomic groups such as the family Saxifragaceae (*in* Soltis and Soltis, 1991), or the genera *Coreopsis* (*in* Cosner and Crawford, 1994), and *Antennaria* (*in* Bayer, 1992), have been the subject of a number of investigations that reveal population genetic relationships among restricted and widespread species.

How has this study contributed to the body of knowledge on genetic variation in rare and endemic plants? First, the results largely conformed with the expectation that restricted species will have less genetic variation than widespread species. Second, the suggestion that genetic variation is as much a function of the individual plant species as of its historical and biological aspects is supported here (i.e., a considerable amount of the genetic diversity within species appears to be independant of genetic and ecological factors). Third, to our knowledge, there have been no studies that have investigated amounts and patterns of genetic variation within a group of phylogenetically unrelated endemic taxa that share the same habitat, such as the endemic plants of the Athabasca sand dunes. The evolution of endemic plants on the Athabasca sand dunes was not a homogeneous process. Sympatric, allopatric, and polyploid speciation have all occurred on the Athabasca sand dunes. The progenitor species to the endemics had both boreal and arctic distributions. Finally, each endemic species investigated was found to reveal its own secrets, and have its own unique history. In this respect, our research suggests one must be careful not to make broad generalizations about restricted species without adequate knowledge of other biological and historical factors. The complete picture of evolution on the Athabasca sand dunes, however, awaits further research.

Future Research. This study has revealed insights into the origin, evolution and conservation of genetic diversity of five endemic plant taxa from the Athabasca sand dunes. Yet, there is still much to be discovered about these and other endemic plants, coined an "evolutionary puzzle" by Rowe and Abouguendia (1982).

There are endemic taxa (*Lechea intermedia* Leggett var. *depauperata* Hodgdon, *Silene acaulis* L. f. *athabascensis*, *Salix brachycarpa* Nutt. var. *psammophila* Raup, *Salix planifolia* Pursh. subsp. *tyrrellii* (Raup) Argus, *Salix turnorii* Raup, and *Tanacetum huronense* Nutt. var. *floccossum* Raup) for which we have no population genetic information. Additional research in this area would contribute information on important factors in the evolution of these endemics and help identify progenitor species from which the endemics have evolved. Investigations of quantitative genetic variation in endemics and related progenitor populations would further reveal the nature of strong directional selection for sand dune adapted traits, genetic bottlenecks, and/or genetic drift in structuring the genetic diversity present in these taxa.

Tomentose leaves and stems, thick leaves that are heavily cuticularized, and rapid stem elongation are characters, possessed by a number of the endemics, that are considered adaptive to active sand dune environments. Do these characters confer higher fitness to individuals on the sand dunes? How is transpiration affected by tomentose or thick cuticularized leaves in an open windy environment? How does stem elongation differ between endemic and progenitor species? In *Stellaria arenicola*, is the yellow capsule an adaptation to reduce heat stress in the developing seeds? Are high selection coefficients keeping sympatric populations of *Deschampsia cespitosa*, *Salix planifolia*, and *Stellaria longipes* from invading the active sand dunes? Studies that address these and other genecological and ecophysiological questions would increase our understanding of the nature of adaptation and evolution of endemic plants on the Athabasca sand dunes.

Recently, interest in exploiting the endemic plants of the Athabasca sand dunes for reclamation of disturbed sandy environments in the boreal forest has been expressed. SYNCRUDE of Fort McMurray in northern Alberta produces large expanses of sandy tailings as a result of heavy oil extraction from the Athabasca tar sands. They have had difficulty reestablishing vegetation in disturbed landscapes and are currently investigating the use of Athabasca sand dune endemic plants for reclamation purposes. Thus, further ecological and genetic research would not only expand our knowledge on the evolution of the Athabasca sand dune endemics, but might have important economic implications for industrial users of sandy habitats in the boreal forest.

Conservation. Studies of restricted species are of interest to evolutionary biologists because rapid evolution often takes place in small isolated populations (Wright, 1931; Nei, Maruyama, and Chakraborty, 1975; Grant, 1981). More recently, information about the ecology and genetics of these taxa has been of interest to the managers of these rare species (Frankel and Soulé, 1981; Falk and Holsinger, 1991).

Why should genetics be important in conservation biology? There are at least three reasons. The fundamental theorem of natural selection suggests the rate of evolutionary change in a population is proportional to the amount of genetic diversity available (Fisher, 1930). Essentially, loss of genetic diversity reduces future evolutionary options. Second, it is generally accepted that heterozygosity, or high genetic variation within populations, is positively related to fitness (Huenneke, 1991). Third, the global pool of genetic diversity represents all the information for all biological processes on the planet (Meffe and Carroll, 1994). In the words of Thomas Foose (1983), "gene pools are becoming diminished and fragmented into gene puddles." Since evolution is the single most unifying concept in all of biology, Vrijenhoek (1989) suggested the placement of the long-term evolutionary perspective at the center of conservation.

How do these concepts translate into the management of rare species? If the evolutionary perspective is important, then a major goal of genetic management should be to allow continued evolutionary change in populations and species of concern. Second, if this perspective is correct, then the population should be the unit of conservation, as it is within populations that genetic changes over generations, and local adaptation, occur. Lastly, there are differing time scales of concern: maintaining viable populations in the short term (extinction avoidance), maintaining the ability for adaptive evolutionary change, and maintaining the capacity for continued speciation (Meffe and Carroll, 1994). While reduction in genetic diversity in declining species is an ultimate factor of concern to the evolutionary-conservation ethic, we must not forget that it is a proximal consequence of habitat destruction, fragmentation, and degradation, which are ultimate factors in most species declines in recent times.

What are the conservation genetic concerns for the endemic plants of the Athabasca sand dunes? With the designation of the 2,000 km^2 Athabasca Sand Dune Wilderness Provincial Park encompassing the entire Athabasca sand dunes in 1992, much has been accomplished to ensure the long-term preservation of the sand dunes, the preservation of the endemic species, and the capacity for continued speciation in the area. We know the endemics have less genetic variation than related species and, presumably, have a reduced capacity for future evolution. However, their abundance on the sand dunes suggests most are well adapted to current environmental conditions. There is no evidence to suggest that populations of the endemics are declining, as investigation of sites that were collected previously in the 1930's by Hugh Raup, and the 1960's and 1970's by George Argus and others, still have viable populations of endemic plants. Thus, the short term concern of maintaining viable populations of the Athabasca sand dune endemics is not a problem.

Many of the conservation genetic concerns are species-specific; some have been mentioned previously. The main threat to *Stellaria arenicola* would be if gene flow with the progenitor *S. longipes* were to increase to a level obscuring the morphological and ecological distinction between the two. Previous studies had indicated, however, that strong selection pressure is keeping the progenitor genotypes from establishing on the harsher active sand dune environment (Macdonald et al., 1987). The polyploid speciation and genetic isolation of *Deschampsia mackenzieana*, left this endemic genetically depauperate. We concluded *D. mackenzieana* had a reduced capacity for future evolution, unless opportunities arise for the immigration of new allelic diversity into future populations. Yet, *D. mackenzieana* is one of the most important sand dune stabilizing species on the Athabasca sand dunes (Raup and Argus, 1982), and appears well adapted to the active sand dune habitat.

Populations that have rare alleles are important, even though these alleles probably confer no fitness advantage, as the preservation of these alleles and those linked to them may ultimately affect the long-term survival of the species. A complete discussion of endemic populations with rare alleles would be quite lengthy, and can be found elsewhere (Purdy and Bayer, in preparation).

A hierarchical analysis of genetic diversity (Nei, 1973) partitions overall genetic diversity into within-population and among-population components, the latter of which can be further subdivided. Despite the proximity of all populations of the endemics to one another, we found a relatively high amount of the total gene diversity apportioned among populations (G_{ST}) for *Stellaria arenicola*, *Deschampsia mackenzieana*, and *Salix silicicola*. As G_{ST} values increase, the preservation of more populations becomes important. Much of this genetic diversity was apportioned among dune fields, emphasizing the importance of protecting the entire Athabasca sand dunes. An analysis of our data indicates that the William River, Thomson Bay, and Yakow Lake dune fields, which are the largest dune fields, harbor most of the genetic variation found within the Athabasca sand dune endemics. These large dune fields, which possess most of the genetic variation within the endemics studied here, also harbor the greatest diversity of endemic taxa, hence, these areas are where future conservation efforts should be concentrated.

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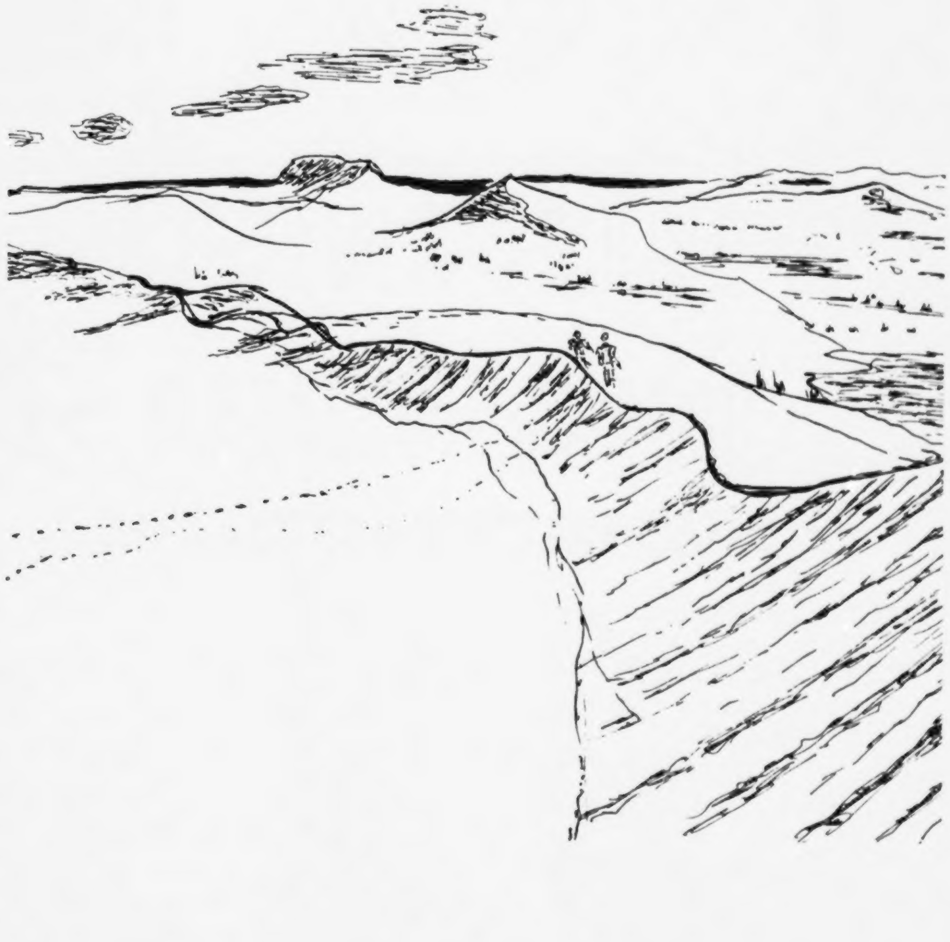

APPENDIX

Glossary [1]

allele Any of the different forms of a gene occupying the same locus.

allopatric Used of populations, species, or taxa occupying different and disjunct geographical areas.

allopolyploid A polyploid hybrid having chromosome sets derived from two different parents.

allozyme The various forms of an enzyme which have the same activity but which differ slightly in amino acid sequence, produced by different alleles at a single locus.

autopolyploid A polyploid variety resulting from the multiplication of the chromosome set of a single species.

breeding system The mode, pattern, and extent to which individuals interbreed with others from the same or different taxa.

cuticularized The presence of a cuticle (waxy layer) on the surface of leaves.

depauperate Impoverished, moribund.

derivative species A species which has evolved from another usually more widespread species.

diploid Having a double set of homologous chromosomes, typical of most organisms.

ecological amplitude The range of a given environmental factor over which an organism or process can function; range of conditions.

ecological race Ecotype; a local race of a species having conspicuous adaptive characters correlated with a given habitat type.

electrophoresis A technique for separating mixtures of organic molecules based on their different rates of travel in an electric field.

endemic Native to, and restricted to, a particular geographical region.

founder effect That only a small fraction of the genetic variation of a parent species is present in the small number of founder members of a new colony or population.

geitonogamy Fertilization between different flowers of the same plant.

gene flow The exchange of genetic factors within and between populations by interbreeding or migration.

gene pool The total genetic material of a freely interbreeding population at a given time.

genetic bottleneck A conceptual occurrence of genetic drift in populations reduced in size through fluctuations in abundance.

genetic diversity The amount and pattern of variation in alleles of genes within and among populations of species or taxon.

genetic drift The occurrence of random changes in gene frequencies of small isolated populations, not due to selection, mutation, or immigration.

genetic identity For a locus, the probability that two gametes chosen at random from two populations carry the same allele relative to gametes and alleles chosen from their own population.

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[1] This glossary is not intended to be a comprehensive dictionary of the terminology used in this thesis. For more information consult "A dictionary of ecology, evolution, and systematics" by R. J. Lincoln, G. A. Boxshall, and P. F. Clark, published by Cambridge University Press, Cambridge, U. K. in 1982.

genetic variation The amount and pattern of variation in alleles of genes within and among populations of species or taxon.

heterozygous Having two different alleles at a given locus.

holocene A geological epoch within the Quaternary period (*ca.* 10,000 B.P. to the present time).

homozygous Having identical alleles at a given locus.

hybridization Any crossing of individuals of different genetic composition, typically belonging to separate species.

inbreeding Mating or crossing between individuals more closely related than average pairs in the population.

indumentum A dense or sparse covering of hairs.

isozyme Any one of the multiple forms of a given enzyme, each with different kinetic properties, that are coded by different genes.

locus (loci pl.) The position of a given gene on a chromosome.

monomorphic With respect to a particular locus, all individuals having the same allele for that locus in a population.

natural selection The non-random and differential reproduction of different genotypes acting to preserve favorable variants and eliminate less favorable variants; viewed as the creative force that directs the course of evolution.

phenotypic plasticity The capacity for the marked variation in the phenotype as a result of environmental influences on the genotype.

polyploid Having more than two sets of homologous chromosomes.

population All individuals of one or more species in a prescribed area.

population genetics The study of gene frequencies and selection pressures in populations.

progenitor An ancestor.

protandry Pertaining to a hermaphroditic organism that assumes a functional male condition during development before reversal to a functional female state.

rare species Geographic distribution (wide, narrow), habitat specificity (broad, restricted), and local population size (large, small) are three traits that are combined to describe seven forms of rarity. In this thesis, rarity typically describes a narrow geographic distribution..

RAPD Randomly amplified polymorphic DNA, a technique where 10 base pair primers are used to amplify DNA in a PCR (polymerase chain reaction) machine to produce DNA strands of variable length.

species A contentious subject, in this thesis we used the evolutionary species concept. A lineage evolving separately from others and possessing its own evolutionary roles and tendencies.

sympatric Used of populations, species, or taxa occurring together in the same geographical area.

taxon (taxa pl.) A taxonomic group of any rank, including all the subordinate groups; any group of organisms, populations, or taxa considered distinct from other such groups.

tetraploid A polyploid having four sets of homologous chromosomes.

tomentose Describing a surface densely covered in short hairs.

vestiture The epidermal covering of a plant, collectively describing a surface densely covered in short hairs.

Curriculum Vitae

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Research Interests:

1. Patterns of variation (morphological, isozymes, DNA) in natural populations, especially related, geographically widespread and restricted taxa.
2. Conservation biology - the effects of habitat loss or change on patterns of biodiversity with an emphasis presently on genetic diversity.
3. Genetic variation in recently colonized landscapes, a measure of the evolutionary potential of northern species.
4. Historical and ecological factors responsible for endemism from populations to ecosystems.

Education:

1987	BSc. (with distinction) Botany, University of Calgary
1990-1995	Ph.D. in Botany (Population Biology). University of Alberta. *Thesis title: Genetic diversity in the endemic plants of the Athabasca sand dunes: origin, evolution, and implications for conservation.*

Awards:

1992/93/94	-Queen Elizabeth II Doctoral Fellowship in Environmental Studies, Alberta Heritage Scholarship Fund (value: $20,000, 2 awarded annually). -Walter Johns Scholarship ($3,000)
1992	-University of Alberta Graduate Teaching Award (Faculty of Science). -NSERC PGS4 Graduate Scholarship (award not taken).
1987	-NSERC PGS1 Graduate Scholarship.
1985/86	-NSERC Summer Undergraduate Scholarship.
1984/85/86	-Louise McKinney Undergraduate Scholarship, Alberta Heritage Scholarship Fund.

Research Grants:

1991-1993 Endangered Species Recovery Fund (World Wildlife Fund of Canada) - Genetic variation in the endemic plants of the Athabasca sand dunes: implications for conservation. $10,000. One of a few botanical projects funded by the WWF to date.

1991-1993 Canadian Circumpolar Institute - Field expenses on the Athabasca sand dunes. $7575.

1985-1986 Department of Indian and Northern Affairs (NSTP grant) - Field expenses for research on the Athabasca sand dunes. $2000.

Refereed Scientific Publications:

Macdonald, S. E., C. C. Chinnappa, D. M. Reid, and **B. G. Purdy**. 1987. Population differentiation of the *Stellaria longipes* complex within Saskatchewan's Athabasca sand dunes. *Canadian Journal of Botany* 65: 1726-1732.

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Reports:

Purdy, B. G. and S. E. Macdonald. 1991. The status of *Stellaria arenicola* (sand stitchwort) a vulnerable species in Canada. Report to the Committee on the Status of Endangered Wildlife in Canada (COSEWIC).

Employment:

1988-1990. Lab assistant for Dr. R. J. Bayer. Genetic analysis of live plant material (isozymes), statistical analysis of data, preparation and handling of herbarium plant specimens, the maintenance of live plant collections, extensive plant collections (live and herbarium) throughout western North America (Alaska to New Mexico).

1988. Field assistant with Canadian Forestry Service, Northern Forestry Centre, Edmonton. Plant identification, ecological site classification, stand productivity analysis, air photo interpretation, and assessment of seedling establishment in herbicide treated cutblocks.

May 1987-March 1988. Department of Biological Sciences, Botany Division, University of Calgary, Alberta. Enrolled in MSc. program. Reproductive biology and phenotypic plasticity in diploid and tetraploid *Stellaria longipes*. Withdrew March 1988 for medical and personal reasons.

1986, 1985. Summer student for Dr. C. C. Chinnappa, University of Calgary, Department of Biological Sciences. Ecological and genetic studies on chickweed (*Stellaria longipes*), extensive travel in the Yukon-Alaska region for plant collections and the maintenance of isolated field camps to study the ecology of endemic plant species from Saskatchewan's Athabasca sand dunes.

Teaching Experience:

1994/95 - Instructor. Conservation and Management of Endangered Species (ENCS 464). This course covered all aspects of the principles and practices of managing and maintaining biodiversity, in particular endangered species. I revised the content of the course considerably from previous years.

1990/91 - Graduate Teaching Assistant. The courses involved lab setup, prelab lectures, preparation of quizzes and exams, and the marking of exams and reports.
- Introductory Botany (BOT199).
- Plant Systematics (BOT220).
- Ecology for Agriculture and Forestry (BOT130).

Guest Lectures:

- Wildlife Conservation (ZOOL460), endangered spaces. 1994/93.
- Man and the Biosphere (ZOOL260), endangered species. 1993.
- Advanced Systematics (BOT520), ribosomal DNA and molecular systematics. 1992.
- Plant Systematics (BOT 220), characteristics of families and orders in the Asteridae. 1991.

Committees and Positions:

1991-present - Director, Alberta Wilderness Association (AWA).
- Alberta Environment Network (AEN) and Alberta Forest Products Association (AFPA) Round TABLE.

1992-present - Chair, Northern Alberta Wilderness Association (NAWA).
- Co-chair, wilderness caucus, Alberta Environment Network.
- Lakeland Provincial Park (Public Advisory Committee)

1989-1992 - Vice-Chair, Northern Alberta Wilderness Association (NAWA).

Invited Talks:

"Botanic gardens, biodiversity, and rare plant conservation". Devonian Botanic Garden, Edmonton, Alberta. 1994.

"The Athabasca sand dunes in northern Saskatchewan: Plants, parks, and people." Regional Student Conference for Northern Studies, Canadian Circumpolar Institute, Edmonton, Alberta. 1992.

"Perspectives on the management of endangered spaces and endangered species: The Athabasca sand dunes." Canadian Circumpolar Institute, University of Alberta. 1992.

"Endangered Spaces Progress Report - The mixedwood boreal forest natural region." CPAWS, AWA, and WWF sponsored talks on the Endangered Spaces Campaign. Edmonton. 1991.

"Lakeland - Opportunities for preservation in boreal Alberta." CPAWS, AWA, and Federation of Alberta Naturalists (FAN). Provincial Museum, Edmonton, Alberta. 1991.

"The Athabasca sand dunes in Saskatchewan: a natural history perspective." Arctic Institute of North America. University of Calgary. 1986.

Conference Presentations:

Purdy, B. G. and R. J. Bayer. 1995. Genetic diversity in the endemic plants of the Athabasca sand dunes: origin, evolution, and implications for conservation. Society for the Study of Evolution, Society of Systematic Biologists, and American Naturalist Society Joint Meeting. Montreal.

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Macdonald, S. E., **B. G. Purdy**, and C. C. Chinnappa. 1988. Isozyme variability and outcrossing rates in the sand dune endemic, *Stellaria arenicola*, and its progenitor *S. longipes*. Canadian Botanical Association Meeting. Victoria.

Chinnappa, C. C., S. E. Macdonald, and **B. G. Purdy**. 1986. Population differentiation of the *Stellaria longipes* complex within an isolated sand dune habitat. International Organization of Plant Biosystematists- Symposium on differentiation patterns in higher plants. Zurich, Switzerland.

Affiliations:

Canadian Botanical Association, Botanical Society of America, American Society of Plant Systematics, Alberta Native Plant Council, Society of Conservation Biology, Alberta Wilderness Association, Canadian Parks and Wilderness Society, Alberta Environment Network.

Other Professional Activities:

1) Updates of wilderness conservation activities in Northern Alberta for the bimonthly Alberta Environment Network News and for the quarterly Wilderness Alberta, a publication of the Alberta Wilderness Association.
2) Presentations at public meetings on issues that relate to parks, wilderness, and sustainable land use.
3) I have been involved in a number of radio, television, and newspaper interviews for conservation groups over the past 5 years.

***References*:**

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